THE MUTTON SNAPPER (*Lutjanus analis*) SPAWNING AGGREGATION FISHERY AT GLADDEN SPIT, BELIZE: INTER-ANNUAL AND WITHIN-SEASON DYNAMICS

A Dissertation

by

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ABSTRACT

Artisanal fisheries constitute a considerable source of employment, income, and protein for many coastal communities in the Caribbean. One of the region's most valuable fisheries is for mutton snapper (*Lutjanus analis*), a coral-reef fish that uses various habitats throughout its life cycle, aggregates to spawn at specific places and times, and is considered vulnerable to extinction. This dissertation focuses on the mutton snapper spawning aggregation fishery at Gladden Spit, Belize (western Caribbean), which has existed since the 1950s. In 2000, the Government of Belize partnered with a community-based nongovernment organization, fishers, and other stakeholders to conserve and co-manage the artisanal fishery. Considering the study fishery as an adaptive socio-environmental fisher-fish system, this dissertation uses a holistic approach to provide baseline socioeconomic and biological information for strengthening conservation and management of mutton snapper fisheries in Belize, applicable to the rest of the Caribbean. The three overall goals of this dissertation were to 1) present the history of the fishery and delineate for the first time its socio-environmental development and impact on inter-annual catch dynamics and yields, using published and grey literature, knowledge of experienced fishers and stakeholders, and data from landings surveys; 2) characterize the fishery's within-season dynamics in 2011 through analyses of the variability in fishing activity, catch and bycatch, and in size, age, and maturation of reproductive mutton snapper, and 3) evaluate the potential distribution of habitat for early life stages of mutton snapper across the Belize shelf, using a GIS-based multi-criteria modeling approach evaluated in the field. Inter-annual analyses evidenced a considerable reduction in total landings and fishing effort of the fishery in the late 1980s, parallel to a rapid growth in the tourism industry and to a shift in the livelihoods of many local fishers. Between 1999 and 2011, during the co-management period of the fishery, relatively stable values of annual catch per unit effort (CPUE), individual sizes, and sex ratios suggested persistence of the fishery. Otolith, size, and gonad analyses depicted, for the first time for the species, age-, size-, and maturation-structured mutton snapper spawning aggregations. Within-season analyses showed how mutton snapper size, age, and degree of maturation vary in relation to the lunar cycle and throughout the spawning season, with individuals significantly smaller and females mostly immature later in the season. Overall, the within-season dynamics of the fishery were influenced by the lunar and seasonal patterns in the reproductive biology of mutton snapper, interactions with co-occurring fisheries, and the experience and traditions of local fishers. The GIS-based model provided a common spatial framework for guiding conservation and spatial management of mutton snapper in Belize and highlighted a low degree of protection currently afforded to critical juvenile habitats constituted of mangroves and seagrass from coastal and shelf regions.

DEDICATION

This work is dedicated to Amrei Baumgarten Peter, my wife and perpetual mentor in science, and to Matthias Granados Baumgarten, our son and mentor in life.

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CHAPTER I

GENERAL INTRODUCTION

Small-scale fisheries in the Caribbean are associated with ecologically complex and extremely vulnerable coral reef ecosystems (Munro, 1983; Salas et al., 2011; Gardner et al., 2003). They also employ nearly 200,000 persons, earn US$5-6 billion annually in foreign exchange, and provide around 10% of the protein intake in the region (Nurse, 2011). Because of their concentrated high biodiversity and spatial heterogeneity (Medley et al., 1993), and because of their multi-cultural use across the region, Caribbean fisheries are typically multi-gear, multi-species, and labor intensive (Salas et al., 2007, 2011). They are also faced with resource overexploitation, complex fleet interactions, and post-harvest problems such as the lack of infrastructure for appropriate processing and marketing (Salas and Gaertner, 2004; Salas et al., 2004; Monroy et al., 2010). Moreover, these fisheries are characterized by many dispersed landing sites, exacerbating the problem of an already limited institutional capacity for effective data collection and analysis of fishery statistics (Salas et al., 2011; FAO, 2012; Heyman and Granados-Dieseldorff, 2012).

Snappers (family Lutjanidae) have historically been among the most economically important small-scale reef fisheries of the subtropical and tropical waters of the western Atlantic, including the Caribbean (Munro, 1983; Allen, 1985; Munro, 1987; Claro and Lindeman, 2004). In the late 1990s, snapper fisheries in the Caribbean yielded mean annual productions of 70,000-75,000 t (Claro and Lindeman, 2004). Because snappers share habitats with other commercially important fishes throughout their ontogenic development, they are often exploited as a part of multi-species fisheries (Lindeman et al., 2000; Claro et al. 2001; Frédou et al., 2006). However, several snapper species are considered highly vulnerable to overexploitation because they are top-carnivore, long-lived, and slow-maturing fishes (Thompson and Munro, 1983; Claro et al., 2001; Frédou et al., 2009a). Sustainability of snapper fisheries is also threatened by uncontrolled fishing pressure, weak fisheries management, and degradation of habitats that are critical for various life-history stages (Pauly et al., 1996; Claro et al., 2009; Freitas et al., 2011).

Throughout the western Atlantic, mutton snapper (*Lutjanus analis* Cuvier 1828) is a highly valuable commercial and recreational reef fish (Claro, 1981; Allen, 1985; Claro and Lindeman, 2004). In the early 2000's, region-wide commercial annual yields were highest in Cuba (900 t; Claro and Lindeman, 2004) and the USA (300 t; SEDAR, 2008). Juveniles inhabit inland estuaries, mangroves, and seagrass beds, while adults inhabit mid-shelf coral reefs and migrate to spawn offshore in dense spawning aggregations following seasonal and lunar cycles (Claro, 1981; García-Cagidae et al., 2001; Heyman and Kjerfve, 2008). Because of the potential threats from uncontrolled harvest of their spawning aggregations, mutton snapper is considered vulnerable to extinction by the International Union for Conservation of Nature and Natural Resources (IUCN; Huntsman, 1996).

Historical declines in spawning aggregation fisheries across the Caribbean, mainly grouper (family Epinephelidae) fisheries, have highlighted the need for protecting these fisheries and for regulating their regional and global markets (Domeier and Colin, 1997; Sadovy De Mitcheson et al., 2008; Sadovy De Mitcheson and Erisman, 2012). However, many of the ecological dynamics of spawning aggregations are still unclear (Sadovy De Mitcheson et al., 2008). Moreover, their response to fishing pressure remains poorly understood. Faced with the lack of adequate fishery statistics and comprehensive ecological studies, management approaches to fish spawning aggregation fisheries in the Caribbean and rest of the tropics have gone from data-poor (*sensu* Honey et al., 2010) to predominantly "data-less" (*sensu*, Johannes, 1998), prompting the adoption of precautionary strategies such as the establishment of marine protected areas while more information for their conservation and management becomes available.

In the western Caribbean, Belize has historically harbored productive reef fisheries (Fiedler et al., 1943; Thompson, 1944; Craig, 1966; FAO, 1968; Koslow et al., 1994). Belize shares the Mesoamerican Barrier Reef with Mexico to the north and the Gulf of Honduras with Guatemala and Honduras in the south (Fig. A.1.1). Faced with an increasing fishing pressure from foreign vessels since the 1980s (Key, 2002; Gibson et al., 2004; Heyman and Granados-Dieseldorff, 2012) and with the fragility of fish spawning aggregations that support species of commercial and food importance, the Government of Belize protected 11 of the nation's multi-species spawning aggregation sites along the Barrier Reef by declaring them as non-extractive zones (NTZ) in 2003 (Government of Belize, 2003a, b; Heyman, 2011). Mutton snapper aggregate to spawn in four of these NTZ, including Gladden Spit (Heyman and Kjerfve, 2008; Kobara and Heyman, 2010).

This dissertation focuses on the mutton snapper fishery at Gladden Spit, southern Belize. Gladden Spit is a reef promontory inside the Gladden Spit and Silk Cayes Marine Reserve (GSSCMR) that hosts prime multi-species fish spawning aggregations among which mutton snapper are predominant in biomass (Heyman and Kjerfve, 2008). Artisanal fishers (i.e., those who use traditional fishing methods for targeting fisheries at small scale, for commercial purposes; *sensu* Berkes et al., 2001) from southern Belize have targeted the mutton snapper spawning aggregations at the site around the full moon days of March-June (Heyman and Graham, 2000; Graham et al., 2008), the peak of the mutton snapper reproduction season at Gladden Spit (Heyman and Kjerfve, 2008). Given the conservation importance of the site's multi-species spawning aggregations and the commercial importance of the Gladden Spit mutton snapper fishery for the nation, the Belize Fisheries Department implemented a special co-management agreement with the Southern Environmental Association (SEA, previously known as Friends of Nature) to protect and manage the site's spawning aggregations, its mutton snapper fishery, and concomitant dive tourism (Government of Belize, 2000, 2003a, b; Gibson et al., 2004). Holistic, stakeholder-centered approaches that integrate fisheries ecology and human dynamics, have been proposed for effectively managing data-poor spawning aggregation fisheries (Lindeman et al. 2000; Ault et al. 2005; Erisman et al., 2012). The mutton snapper fishery at Gladden Spit presents a valuable opportunity to holistically assess responses of fish spawning aggregations to fishing and to evaluate approaches to adaptive co-management of artisanal fisheries. Moreover, basic biological and fishery data for its management and long-term monitoring are still needed in Belize. By considering the mutton snapper fishery at Gladden Spit as a socio-environmental fisher-fish system that has adaptively responded to 1) the ecology of the species at the site, 2) the artisanal dynamics of fishers, and 3) the fishery conservation and management constituencies and mechanisms that have been adaptively reviewed and implemented by co-managers and stakeholders, this dissertation used a pioneering holistic approach to provide baseline socioeconomic and biological information for strengthening conservation and management of mutton snapper fisheries in Belize, applicable to the rest of the Caribbean. The three overall goals of this dissertation were to 1) delineate the history of the fishery and present a retrospective analysis of its inter-annual dynamics within its socio-environmental context (Chapter II), 2) characterize the fishery's within-season dynamics (Chapter III), and 3) evaluate the potential distribution of habitat for early life stages of mutton snapper across the Belize shelf (Chapter IV).

With the exception of a short-term study (Graham et al., 2008), a comprehensive evaluation of the history of the mutton snapper fishery at Gladden Spit does not exist. Therefore, in Chapter II, I was interested in 1) identifying long-term trends in the fishing history with reconstruction of annual catches and estimation of fleet size since the late 1980s; 2) comparing inter-annual trends in catch per unit effort (CPUE) and in fish sizes for the last decade (1999-2011); and 3) delineating possible factors that might have caused the observed trends in annual catches, including social changes, environmental and biological factors, and management measures. To accomplish this, I used information gathered from fishery landings surveys, national fisheries statistics reports, published and grey literature, and expert knowledge of fishers and stakeholders.

Given that fishers have traditionally targeted the mutton snapper spawning aggregations at Gladden Spit during the peak of their reproduction period, it is possible to use their landings for assessing the size and age structures of reproductive mutton snapper, as well as their degree of maturation. This is also an exceptional opportunity because fishing (commercial or scientific) of mutton snapper spawning aggregations is banned in the rest of the Belize Barrier Reef and restricted in several locales across the species distribution range. This basic, yet missing, biological information can be used as a baseline for the long-term monitoring of the fishery at Gladden Spit and used to inform management of other mutton snapper fisheries across the western Atlantic. Landings surveys can also be used to describe the mutton snapper fishery's fleet dynamics and to evaluate interactions with co-occurring nontarget species (i.e, bycatch species) at Gladden Spit. This is important because, in addition to biological factors and catch statistics, scientists and managers need to consider technological issues that also affect fisheries dynamics (Murawski, 1984; Arreguín-Sánchez, 1996; Ward, 2008). Indeed, differences in fishing practices and fleets that interact in shared fishing grounds affect fishing effort, the overall catch efficiency, and hence, the corresponding yields (Salas and Gaertner, 2004; Salas et al., 2004; Frédou et al., 2009b; Monroy et al., 2010). Thus, in chapter III, I was interested in 1) characterizing the within-season fishing practices and landings dynamics of the mutton snapper fishery at Gladden Spit and its associated bycatch using fishing-fleet and catch-based data; 2) documenting the size and age structures, as well as the degree of maturation of reproductive individuals through analyses of otolith microstructure, individual length, and gonad state; 3) testing whether individual size, age, and degree of maturation varied in relation to the lunar cycle and among months of the peak spawning season; and 4) testing whether the fishing fleet and bycatch species composition changed among months.

Since chapters II and III address adult stages of mutton snapper, Chapter IV focused on the juvenile life-history stages in order to holistically assess conservation and management of the species in Gladden Spit and rest of the Belize shelf. Biological and oceanic factors, as well as coastal development and fishing pressure, impact multiple life-history stages of Caribbean reef fishes and therefore affect the size of their populations (Bohnsack and Ault, 1996; Lindeman et al., 2000; Claro et al., 2009). Moreover, variability in juvenile habitat quality, availability, and connectivity can regulate the size of fish populations (Forrester, 1990; Holbrook et al., 2000; Secor and Rooker, 2005). Thus, in Chapter IV, I evaluated the potential distribution of suitable habitat for juvenile mutton snapper in Belize and assessed the degree of protection afforded to these habitats using a GIS-based multi-criteria modeling approach.

CHAPTER II

HISTORY AND INTER-ANNUAL DYNAMICS OF THE MUTTON SNAPPER (*Lutjanus analis*) SPAWNING AGGREGATION FISHERY AT GLADDEN SPIT, BELIZE[*]

2.1. Introduction

Snappers (family Lutjanidae) have historically been among the most economically important reef fisheries of the Caribbean (Munro, 1983; Pauly et al., 1996; Salas et al., 2007). Throughout their ontogenetic development, they use coastal and open-water habitats and are often exploited as multi-species fisheries of peculiar seasonality at different locations, including fish spawning aggregations sites (Lindeman et al., 2000; Claro et al. 2001; Claro and Lindeman, 2003). Typical Caribbean fisheries, they are largely artisanal (i.e., those pursued in small scale for commercial purposes, using traditional fishing methods; *sensu* Berkes et al., 2001) and because of their multi-cultural, multi-scale, multi-species, and data-sparse nature, they are difficult to assess and manage using conventional methods (Medley et al., 1993; Pauly et al., 1996; Frédou et al., 2009b). Moreover, uncontrolled fishing pressure, weak fisheries management and law enforcement, piecemeal governance, and degradation of critical life-history habitats

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by natural and anthropogenic stressors continue to threaten their sustainability (Munro, 1983; Claro et al., 2009; Freitas et al., 2011).

Because several snapper species are highly desirable food fish, top carnivores, long-lived, relatively slow to reach reproductive maturity, and aggregate to spawn in highly predictable dense concentrations of individuals, they are considered highly vulnerable to overexploitation (Domeier and Colin, 1997; Claro and Lindeman, 2003; Sadovy and Domeier, 2005). Historical reef fish spawning aggregation declines, mostly grouper (family Epinephelidae) fisheries, have been reported for the Caribbean, highlighting the need for protecting and managing fish spawning aggregations across the region and for regulating their regional and global markets (Pauly et al., 1996; Claro and Lindeman 2003; Sadovy De Mitcheson and Erisman, 2012). Despite recent progress in the study of Caribbean fish spawning aggregations, many of their ecological and behavioral dynamics are still unclear (Sadovy De Mitcheson et al., 2008), and their response to fishing pressure remains poorly understood. As a result, management approaches to fish spawning aggregation fisheries in the region have been predominantly "data-less" (*sensu*, Johannes, 1998), prompting the adoption of precautionary strategies such as the establishment of marine reserves, while more information on the protected resources becomes available.

In the western Caribbean, fishers from Belize, Guatemala, and Honduras have traditionally harvested snappers during spawning aggregations (Craig, 1966; Heyman and Granados-Dieseldorff, 2012). Gladden Spit, a reef promontory in the southern Belize Reef and a multi-species reef fish spawning aggregation site (Heyman and Kjerfve, 2008), has been known as a productive ground for snapper artisanal fisheries since the 1950s (Bradley, 1956 in Craig, 1966). Mutton snapper (*Lutjanus analis* Cuvier 1828) fisheries from the area have prevailed in national finfish yields since the 1990s (Koslow et al., 1994; Auil et al., 1999). The biological richness and tourism values of the Gladden Spit area, as well as the plea for regulation of illegal fishing and poaching (Heyman and Graham, 2000; Heyman, 2011), led the Government of Belize to declare the Gladden Spit and Silk Cayes Marine Reserve (GSSCMR) in 2000 (Government of Belize, 2000). As part of a network of marine reserves and protected spawning aggregation sites throughout the nation (Fig. A.1.2.), GSSCMR is currently co-managed by the Belize Fisheries Department and the community-based nongovernment organization Southern Environmental Association (SEA).

The artisanal mutton snapper fishery at Gladden Spit presents a valuable opportunity to assess responses of fish spawning aggregations to fishing and to evaluate approaches to adaptive co-management of artisanal fisheries. With the exception of a short-term study (Graham et al., 2008), a comprehensive evaluation of the history of this fishery does not exist. In response and in the interest of expanding baseline information for the adaptive co-management of the artisanal mutton snapper fishery at Gladden Spit, this chapter presents a retrospective analysis of the history of the fishery in its environmental and socioeconomic context. Using information gathered from fishery landings surveys conducted by the co-managers in the area, as well as from national fisheries statistics reports, published and grey literature, and knowledge of experienced fishers and expert stakeholders (*sensu* Grant and Berkes, 2007), I was able to 1) delineate the history of the fishery (1950-2011); 2) identify long-term trends in yields with reconstruction of annual catches and estimation of fleet size since the late 1980s; 3) compare inter-annual trends in underwater fish abundance, catch per unit effort (CPUE), and in fish length and weight at harvest for the last decade (1999-2011); and 4) delineate possible factors that might have caused the observed trends in the fishery, including social changes, environmental and biological factors, and management measures.

2.2. Material and methods

2.2.1. Study species

Mutton snapper (*Lutjanus analis*) is a long-lived, reef-associated fish that occurs across the western Atlantic Basin, from Massachusetts, USA, to Sao Paulo, Brazil, including the Caribbean (Allen, 1985; Mason and Manooch, 1985; Claro and Lindeman, 2004). The species tolerates a wide range of environmental conditions in both the laboratory (Clarke et al., 1997; Watanabe et al., 1998; Watanabe, 2001) and the wild (Claro and Lindeman, 2004). As euryhaline and eurythermal fish, mutton snapper undergo ontogenetic habitat shifts across their different life stages during which they encounter different environmental conditions and predators (e.g., dolphins, sharks, snappers, and other large predatory fishes). Mutton snapper are euryphagic carnivores and prey on various species throughout development. During their settlement and juvenile stages, they use mangrove estuaries and vegetated sandy bottoms. As adults, they migrate offshore to coral reefs and other complex benthic hard habitats for reproduction (Allen, 1985). As gonochoristic fish, they reach sexual maturity as males and females as soon as 3 years (380-450 mm total length -TL), but typically at 4-6 years (500 mm TL) (Claro and Lindeman, 2004). Estimated growth rates and maturation sizes vary across the species range (Mason and Manooch, 1985; Burton, 2002; Claro and Lindeman, 2004). Adult populations have no significant variation in size between sexes and typical populations have sex ratios close to 1:1 (Claro and Lindeman, 2004). The maximum age for the species was assumed to be 29 years (Burton, 2002) until recent estimates raised it to 40 years (SEDAR, 2008).

Mutton snapper are rarely found in groups, except during spawning migration events (Allen, 1985; Claro and Lindeman, 2004). They are classified as a species that spawns in transient fish spawning aggregations (FSAs) (Domeier and Colin, 1997). Mutton snapper FSAs have been documented in Florida (Domeier and Colin, 1997; Watanabe, 2001; Burton, 2002), the Bahamas and Turks and Caicos' Islands (Mueller et al., 1994; Domeier and Colin, 1997), the Cayman Islands (Kobara and Heyman, 2008), Cuba (Claro, 1981; Claro and Lindeman, 2003; Claro et al., 2009), Belize (Heyman et al., 2001; Graham et al., 2008; Heyman and Kjerfve, 2008), Puerto Rico and the U. S. Virgin Islands (Matos-Caraballo et al., 2006a; Carr and Heyman, 2012), and Brazil (Pimentel and Joyeux, 2010; Teixeira et al., 2010; Freitas et al., 2011).

Throughout its geographic range, mutton snapper is a highly valuable species for commercial, recreational, aquaculture, and aquarium purposes (Allen, 1985; Watanabe et al., 1998; Benetti et al., 2002; Claro and Lindeman, 2004). They have been targeted with different fishing methods and gears, including gill nets, hand lines, rod and reel, fish traps, and spear guns, at industrial, recreational, and artisanal scales (Claro and

Lindeman, 2004). Harvestable sizes for the Caribbean range between 300 and 800 mm TL (Claro and Lindeman, 2004). The record size and weight is 940 mm TL and 15.6 kg, respectively, for mutton snapper harvested in Florida waters, United States (Froese and Pauly, 2012).

In contrast to other snappers and different from most groupers, mutton snapper tolerate wide ranges of environmental attributes throughout their ontogenetic development (Allen, 1985; Watanabe, 2001; Claro and Lindeman, 2004). The species has also shown remarkable resistance to fishing pressure across the western Caribbean, including Cuba (Claro and Lindeman, 2004; Claro et al., 2009), Belize (Thompson, 1944; Craig, 1966), and Honduras (Gobert et al., 2005). Indeed, a mutton snapper FSA at Riley's Hump in the Florida Keys was able to rebuild after appropriate management was put in place (Burton, 2002; Burton et al., 2005). Nonetheless, mutton snapper is still considered vulnerable to overfishing and extinction in the medium term (Huntsman, 1996).

2.2.2. Study area

Gladden Spit is a reef promontory adjacent to the 1,000 m isobath where the Belize Barrier Reef bends at ~90^{o}, 40 km east of the village and peninsula of Placencia, Stann Creek District (Figs. A.1.2). The distinctive geomorphology of the site inspired the local names of the "elbow" and "point of reef" (Gibson et al., 2004). A tropical climate influences the region with distinct rainy (June-November) and dry (December-May) seasons and mean monthly seawater temperatures of 27-31^{o} C (Thattai et al., 2003).

Salinity is typically fully oceanic, though it is occasionally reduced by excessive rainfall events such as with the passage of tropical cyclones (Sheng et al., 2007). Details on the meteorology and oceanography at Gladden Spit are described elsewhere (Ezer et al., 2005; Heyman et al., 2005; Ezer et al., 2011).

Gladden Spit harbors multi-species FSAs among which cubera snapper (*Lutjanus cyanopterus*, family Lutjanidae), dog snapper (*Lutjanus jocu*), and mutton snapper are predominantly abundant (Heyman and Kjerfve, 2008). Moreover, Gladden Spit is one of the four active sites where mutton snapper aggregate to spawn along the Belize Barrier Reef (Heyman and Requena, 2002; Kobara and Heyman, 2010). At Gladden Spit, mutton snapper spawn in groups of 20-100 individuals, typically in the afternoon (13:00-15:00 h). This is distinct from most Lutjanids and other transient spawning species that typically spawn at sunset in massive group spawning events (Heyman and Kjerfve, 2008). Moreover, mutton snapper aggregate to spawn at the site between February and September (Heyman and Kjerfve, 2008), similar to other snappers that aggregate most frequently during the warmer months (April-September), but different from groupers that are the dominant spawners at Gladden Spit during the colder months (January-March) (Heyman and Kjerfve, 2008).

The Government of Belize declared the Gladden Spit and Silk Cayes Marine Reserve (GSSCMR) in 2000 (Government of Belize, 2000; Gibson et al., 2004). The declaration of the 105 km^2 multi-use reserve was the product of a long series of community consultations leaded by Friends of Laughing Bird Caye (FOLBC), a community-based nongovernment organization (NGO) based in Placencia (Gibson et al., 2004; Goetze, 2005). Early in 2002, FOLB merged with Friends of Placencia Lagoon to form Friends of Nature (FON), known as the Southern Environmental Association (SEA) since 2009. It was not until 2002, when FON signed a co-management agreement with the Belize Fisheries Department, that GSSCMR started under formal management (Gibson et al., 2004). Since then, an advisory committee consisting of various local and national agencies develops the regulations of the reserve (Government of Belize, 2003a). During periodic community consultations, reserve co-managers, local fishers, tourism operators, board members of fishing cooperatives, and other key stakeholders discuss and review the regulations for GSSCMR, particularly early in the year and in anticipation to the start of the fishing and tourism seasons. Conservation and fisheries management regulations are enforced by SEA and the Belize Fisheries Department in the field through patrols from park rangers and enforcement staff who are members of the local fishing communities.

The Gladden Spit and Silk Cayes Marine Reserve has three zones with various levels of protection (Fig. A.1.3): the General Use Zone (GUZ), the No Take Zone (NTZ - Conservation Zone 1), and the Restoration and Spawning Area (Conservation Zone 2) (Government of Belize, 2003a). Fishers with a national commercial fishing license are permitted to fish within the GUZ. The FSA site in which the primary mutton snapper fishery occurs is located within the Restoration and Spawning Area Zone that opens for limited traditional fishing only from March to June every year (see following section).

2.2.3. Study fishery

The mutton snapper fishery at Gladden Spit can be considered as a socio-environmental fisher-fish system (*sensu* Armitage et al., 2009; Ostrom, 2009) that has adaptively responded to 1) the ecology of mutton snapper at Gladden Spit, 2) the artisanal dynamics of fishers, and 3) the conservation and management constituencies and mechanisms that have been adaptively reviewed and implemented by co-managers and stakeholders since GSSCMR was created (2000).

Using traditional hand lines, fishers from Southern Belize (Placencia and Seine Bight initially, and later from Independence-Mango Creek, Hopkins, and Monkey River; Fig. A.1.2) have for long harvested mutton snapper at Gladden Spit. Every year between March and June, for a period of 10-14 days starting around 2 days prior to full moon, fishers set up base camps on various sand cayes, from which they commute daily 10-15 km to the shelf-edge fishing area (Graham et al., 2008). Buttonwood Caye, the primary base camp and landing site for mutton snapper from Gladden Spit, is mainly used by fishers from Placencia and Independence, while Gladden Caye is mainly used by fishers from Hopkins (Figs. A.1.2 and A.1.3). Fishers land their catches at these camps and clean their product before transporting it to their village cooperatives on the mainland. Typically sold whole, selling price for 1 kg of mutton snapper has varied little, from US$ 2.75 in the 1998-2002 period (Heyman and Graham, 2000; Graham et al., 2008) to US$ 3.50 in 2011 (or US$ 2.87 for 2002, adjusted to the Consumer Price Index of inflation of the US Department of Labor) (this study). The Placencia Producers Cooperative Society

Ltd. (Placencia Cooperative hereafter) has been the major collecting cooperative for mutton snapper from Gladden Spit (Auil, 1994; Auil et al., 1999; Graham et al., 2008).

The spawning aggregation targeted by the mutton snapper fishery occurs along the shelf break in 25-60 m water depth on the forereef slope (Heyman and Kjerfve, 2008). Fishers typically set temporary moorings at the wall edge and cast their baited hooks over the edge of the shelf. Since bigger fish are typically deeper, fishers cast as far over the shelf edge as they can. Traditional hand lines evolved from cotton to nylon monofilament lines, 100-400 lb test, to which 1-3 hooks are attached (participant observation). Each fisher has traditionally used one hand line. In 2011, hand lines were weighted with ~15 cm pieces of 2 cm diameter steel rebar and 5/0 standard hooks were baited with cut mullet (family Mugilidae), shad and sardines (family Engraulidae), queen conch (*Strombus gigas*, family Strombidae), or by-catch species such as grunts (family Haemulidae), porgies (family Sparidae), and triggerfish (family Balistidae).

In 2011, the fishing fleet of mutton snapper at Gladden Spit consisted largely of Mexican-style skiffs (7-7.6 m hull) equipped with four-stroke engines (40-60 hp), and with one to three persons per boat. During fishing hours, fishers store the catch either in coolers (144 x 65 x 66 cm) with freshwater ice, but more often inside old recycled refrigerators (150 x 60 x 65 cm) or customized ice boxes of similar size (Figs. A.1.4A and A.1.4B). At Buttonwood Caye, fish are eviscerated, rinsed, transferred to larger ice boxes, and stored in ice for 2-3 days before being transported inland.

The reserve allows fishing on the aggregation site during two weeks each month between March and June and only during daylight hours (6:30-17:00 h). Fishing is limited to fishers holding special "traditional" fishing licenses for mutton snapper (Government of Belize, 2003a). Fishing licenses are issued by SEA and the Belize Fisheries Department. On a daily basis and following the reserve's regulations, fishers usually leave camp for Gladden Spit at 6:00-6:30 h and return to process their catches up to twice daily. Depending on their half-day harvests, cooler capacity, and amount of ice left while ashore, fishers make one or two trips per day. Boats fishing half day (~4-5 h) in the morning usually land at Buttonwood Caye between 11:30 and 13:00 h. The last boats of the day (fishing either for half-day in the afternoon or full day since the morning hours) land at Buttonwood Caye between 16:00 and 17:30 h.

Fishing effort for mutton snapper at Gladden Spit is highly dependent on the inter-annual periodicity of the lunar cycle and varies in intensity depending on the timing of the full moon during each calendar month of the season (Heyman and Graham, 2000; Graham et al., 2008). It is also dependent on the reproductive behavior of mutton snapper and on the traditions and experience of fishers (Chapter III). Moreover, the fishing season for mutton snapper typically overlaps with both Easter and the start of the highly lucrative lobster (*Panulirus argus*, family Palinuridae) season on June 15 (Chapter III). Since most fishers that target mutton snapper also fish for lobster, they switch to lobster as soon as they can, sometimes foregoing the last (June) mutton snapper spawning event. Typically, if the full moon falls during the last two weeks of the month, March is included as a fishing month for mutton snapper and June is excluded because of the overlap with lobster season. On the other hand, if the moon falls early in the month, both March and June would be fished. During these "early moons", yellowtail snapper

(*Ocyurus chrysurus*, family Lutjanidae) dominate landings from Gladden Spit in March (Chapter III).

2.2.4. Data collection

Data analyzed in this chapter can be divided into two periods: 1) the preceding and historical period of the fishery (1930-1997), and 2) the monitoring and management period of the fishery (1998-2011). Historical reports from international expeditions (e.g., Fiedler et al., 1943; Thompson, 1944) and subsequent studies addressing the snapper fisheries of Belize (Craig, 1966; Auil, 1994; Koslow et al., 1994; Auil et al., 1999; Heyman and Graham, 2000; Zeller et al., 2011) did not include data specific to mutton snapper from Gladden Spit. It was until 1998, when the monitoring of Gladden Spit's FSAs formally began, that mutton snapper catches from the site started to be recorded. Under the supervision of the Belize Fisheries Department, The Nature Conservancy started monitoring Gladden Spit's FSAs through annual underwater visual census (UVC) using SCUBA and included surveys of the mutton snapper landings at Buttonwood Caye (Heyman and Requena, 2002; Gibson et al., 2004). The community-based NGO FON/SEA assumed full responsibility for monitoring in 2006. In parallel, the multi-agency Belize National Spawning Aggregation Working Group formed in 2001 and a national reef FSA monitoring protocol (Heyman et al., 2002, 2004) was later adopted for the country's FSA sites. All the data collected in the field (both landings and UVC data) have been collected in accordance with the national monitoring protocol and maintained in hard copy and digitally in Microsoft Excel spreadsheets or Access databases at FON/SEA.

Following the national monitoring protocol for FSAs, landings data have been collected by teams of 4-6 persons. Landings teams have been mainly constituted of local community researchers and family members of local fishers hired for the survey season. Based on the management plans for GSSCMR, collection of landings data has excluded other landing sites (e.g., Gladden Caye) and other months of the reproduction period of mutton snapper in the area (i.e., February and July-September). Using the Belize "landings" and "CPUE" (catch per unit of effort) data collection forms, landings surveys have combined catch data with socioeconomic and demographic profiles of fishers obtained through semi-structured interviews. Survey data used for this chapter included number of boats landing mutton snapper at Buttonwood Caye in one day, number of hours fished per boat (soak time plus travel time), number of fishers per boat (1-3), number of trips made to Gladden Spit during the day (half-day or full-day), individual fish lengths (commonly TL, mm), weight (lb or kg), and sex (male or female). Demographic and socioeconomic data used in this study included information on fishers' village of residence, type of artisanal fishing method used, boat size (ft), engine power (hp), main selling market or fishing cooperative, and fish buying price (BZ$*$\text{lb}^{-1}$, where 2 BZ$ = 1 US$).

Following the budget and logistics planned for the season and the dynamics of the mutton snapper fishery, landings teams either camp at Buttonwood Caye or reach the caye before 11:00 h, in anticipation of the first boats that might land (i.e., those fishing half day in the morning). Teams attempt to measure all fish landed at the caye all day. Limited by team capacity, particularly by the number of persons collecting data, some boats were not surveyed for landings, especially when all boats landed simultaneously at the end of the day. Also, other situations when boats were not surveyed included boats landing at other cayes, those returning directly to mainland from Gladden Spit, and those eviscerating their catch at sea before landing.

Parallel to landings surveys at Buttonwood Caye, underwater visual censuses (UVC) using SCUBA record species composition, abundance, and behavior of fish aggregating at Gladden Spit (see Heyman et al., 2004). For this study, I used data from UVC surveys that were conducted by teams of 2-4 divers. Ideally, two 30-min monitoring dives are performed daily, before 11:00 h and after 16:30 h, the time period within which mutton snapper are known to spawn at Gladden Spit.

2.2.5. Data compilation and synthesis

2.2.5.1. Preceding and historical period of the fishery (1930 - 1997)

In order to delineate the environmental and socioeconomic history of the mutton snapper fishery at Gladden Spit, I integrated information from historical reports, national statistical reports, social and biological studies, and patriarch fishers' and stakeholder's expert knowledge. Because of their continuous interaction with the environment and the resources, fishers and expert stakeholders (e.g., park rangers, members of fishing cooperatives) maintain a deep understanding of the biology and seasonality of the species they target. In data-sparse situations, such as for the period of this historical analysis, fishers' knowledge can complement scientific research and provide practical information that can be used in management (Pitcher et al., 1998; Johannes et al., 2000; Berkes, 2012). Following this approach, catches before 1998 were reconstructed by combining 1) fishers and expert knowledge for 1985, 2) reports on finfish production from the Placencia Cooperative to the Belize Central Statistical Office (currently known as the Statistical Institute of Belize) for 1988-1990 (Belize Central Statistical Office, 1991, 1994), and 3) finfish yields estimates for the area by Koslow et al. (1994) and Auil et al. (1999) for 1991. For 1985, annual catches for mutton snapper were reconstructed assuming that approximately 50% of the total finfish catches reported by the Placencia Cooperative corresponded to mutton snapper from Gladden Spit, as expressed by several experienced fishers and former cooperative directors. For 1991, Koslow et al. (1994) and Auil et al. (1999) assumed that 74 % of the catch from "The Gladden Caye Area" corresponded to mutton snapper. For 1988-1990, the median of the 1985 and 1991 proportions (i.e., 62%) was used to estimate mutton snapper catches from Gladden Spit from the total finfish yields reported by the Placencia Cooperative.

In order to reconstruct fishing effort and plot annual CPUE (kg*hook-h^{-1}) between 1991 and 2011, I used 1) CPUE data from Koslow et al. (1994) and Auil et al. (1999) for 1991; 2) annual catches and fishing effort for 1999–2011 from SEA's database; 3) total fishing effort and catches estimated for Gladden Spit by Graham et al. (2008) in 2000 and 2001, and 4) information derived from reports of park rangers patrolling Gladden Spit for 2006-2011. For this latter, the number of boats actively fishing at Gladden Spit recorded daily by park rangers allowed to determine the proportion of boats that were not accounted for in landings surveys at Buttonwood Caye. This proportion was used to estimate total fishing effort and catches at Gladden Spit for 2006-2011.

2.2.5.2. Monitoring and management period of the fishery (1998-2011)

In order to characterize trends in landings and UVC abundance, I compiled and synthesized previous and recent field data collected by the co-managers of GSSCMR (1998-2011). Following Stephens and MacCall (2004), I extracted subsets of relevant data from the large database SEA maintains (1998-2009). As the leader of SEA's landings team in 2011, I collected landings data at Buttonwood Caye and estimated UVC fish abundances in collaboration with the divers who surveyed Gladden Spit (March-June 2011). Landings and UVC surveys were not conducted in 2005 and 2010 and data were missing from SEA's database for 2002.

Between 1998 and 2011, the quality and extent of mutton snapper landings data from Gladden Spit was uneven and limited by several factors. As mentioned before, not all the boats fishing at Gladden Spit were accounted for in landings surveys between 1998 and 2011. Moreover, year 1998 was excluded from analyses due to the low sampling effort (n = 2 survey days for the entire year).

Sampling effort (survey days) was first calculated by month (March-June) and by year (1999-2011) from datasets. This allowed me to detect inconsistent sampling effort among months and among years prior to conducting statistical comparisons (Table A.2.1). Considering that the fishing fleet for mutton snapper at Gladden Spit was traditionally comprised of Mexican-style skiffs between 1999 and 2011, I assumed that 1) the maximum fishing effort per boat during an active day was 3 handlines*boat^{-1} for the entire data period, and 2) one boat-day fishing was equivalent to > 8 h of soak time.

Following Malvestuto (1996) and Fabrizio and Richards (1996), catches per boat were first estimated by the total number of fish landed (total catch abundance) and their corresponding weight (total catch weight). Using the total-ratio method, catches were then standardized to catch per unit effort (CPUE) by numbers (fish * boat-days-fishing^{-1}, hereafter referred to as CPUE-Abundance) and by weight (kg * boat-days-fishing^{-1}, hereafter referred to as CPUE-Weight). Though CPUE estimated by weight has traditionally been used in fisheries science, studies recommend also estimating CPUE by abundance since changes in the total biomass of fish caught (i.e., CPUE-Weight) does not necessarily reflect changes in harvested fish abundance (see Branch et al., 2011; Pauly et al., 2013; references therein). Since fishing activity at Gladden Spit follows a traditional lunar periodicity and overlaps with Easter and the lobster season, the total-ratio estimator allowed me to standardize for uneven contributions of daily and monthly fishing effort and to control for variable catchability. For graphical comparison purposes, the estimated CPUEs and fishing effort were normalized to the maximum value obtained during the entire study period and expressed as relative ratios (%) by month and by year.

In order to characterize inter-annual trends (1999-2011) in mutton snapper landings, I used only May data because 1) May is traditionally known as the peak of the mutton snapper fishing season at Gladden Spit; 2) monthly data for March, April, and June were frequently missing from datasets (Table A.2.1); and 3) the fishery catchability and therefore estimates of CPUE-Abundance, CPUE-Weight, fishing effort, and individual size of fish landed at Buttonwood vary significantly within season and with full moon period (Chapter III). Since differences in size between female and male mutton snapper are typically not significant (Claro and Lindeman, 2004), I calculated male:female (M:F) ratios by month and by year and combined individual male and female data for plotting length-weight relationships and length frequency distributions of landed fish.

In order to test for inter-annual changes (1999-2011) in CPUE-abundance, CPUE-weight, and individual fish length and weight, I performed univariate one-way PERMANOVA tests (Permutational MANOVA/ANOVA -Anderson, 2001a; McArdle and Anderson, 2001) in an approach similar to parametric ANOVAs, using PERMANOVA+ (Anderson et al., 2008) in PRIMER (Plymouth Routines In Multivariate Ecological Research) version 6 (Clarke and Gorley, 2006). PERMANOVA is a more versatile and robust non-parametric test (Anderson, 2001b) suitable for the data-sparse situations encountered for this study. As a permutation-based test routine and using resemblance distance measures, PERMANOVA is distribution free and does not assume linearity of response variables nor normally-distributed errors.

PERMANOVA can be conceptualized as a geometrical approach to MANOVA/ANOVA (Anderson, 2001a; McArdle and Anderson, 2001). Under this approach, PERMANOVA works with any distance measure that is appropriate to the data and allows the handling of complex unbalanced designs. As such, the sum of squared distances between points and their geometric centroid is equal to the sum of squared inter-point distances divided by the number of points (Anderson, 2001). In that way, an additive partitioning of sums of squares can be obtained for any distance measured directly from the distance matrix, without calculating the central location of groups (Anderson, 2001a). By using Euclidean distances in PERMANOVA matrices, the computational structure of ANOVA tests is replicated (Anderson et al., 2008). Pseudo-F ratios (analogous to F-ratios in ANOVA) are based on the total sum of squares of the distance matrix and the residual (i.e., within-group) sum of squares for a given group classification. Evaluating the significance of the pseudo-F statistic requires a permutation test. Anderson (2001a) recommends at least 1,000 permutations for a test with $\alpha = 0.05$.

Data were log-transformed (log[x + 1]) to smooth overdispersion of sample sizes (McArdle et al., 1990). For each of the four variables in the analyses, I created Euclidean-distance matrices *a priori* and ran one-way PERMANOVA tests with years as the main effect (see Anderson et al., 2008). Mean-squared errors, pseudo-F ratios, and p-values were obtained from 9,999 permutations ($\alpha = 0.05$). Posterior pair-wise testing of significant year effects (one-way PERMANOVAs: $p \leq 0.05$) were based on comparisons also obtained from 9,999 permutations. Daily CPUE estimates were used as replicates in PERMANOVA designs testing for inter-annual changes in CPUE-Abundance and CPUE-Weight. Daily median values of mutton snapper TL and body weight were used as replicates for testing inter-annual changes in size.

In order to characterize inter-annual trends (1999-2011) in mutton snapper UVC abundance, I plotted the frequency distribution of daily UVC counts and determined the maximum value recorded for each month of the fishing season (March-June). Since mutton snapper remain aggregated at the spawning site until spawning is completed (Claro and Lindeman, 2003), this value (denoted as "peak UVC counts") was used as a proxy of the maximum number of mutton snapper aggregating at Gladden Spit (UVC-Abundance) every month. Although data were derived from 10 years of surveys that amounted >1000 diver-h of UVC, only May months were consistently surveyed and UVC data for 2002, 2005, and 2010 were missing from datasets. UVC-Abundance was normalized to the maximum value and plotted as ratios (%) with normalized CPUE-Abundance and normalized fishing effort for comparison purposes. Because UVC survey methods changed with year, statistical comparisons of annual UVC counts were not possible.

2.3. Results

2.3.1. Preceding and historical period of the fishery (1930-1997)

The preceding and historical period of the mutton snapper spawning aggregation fishery at Gladden Spit could be traced back to the 1930s (Table A.2.2 and Fig. A.1.5). Although there is evidence that pre-Columbian Maya settlements existed along the coast of southern Belize (Mackinnon and May, 1990), it was until the second half of the 19th century, after the decline of the mahogany industry, that the Placencia peninsula (Fig. A.1.1) was colonized. The Garifuna village of Seine Bight was established in 1869 and was dedicated to agriculture and animal husbandry (Key, 2002). The Creole village of Placencia was formally established as a fishing community in 1936 (Key, 2002). During those times, when Belize was still known as "British Honduras", most fishing activity was concentrated in the northern part of the country (Thompson, 1944; Craig, 1966). The commercial fishing industry of Belize, predominantly small scale, focused on the export of spiny lobster and queen conch (Thompson, 1944; FAO, 1968; King, 1997; Huitric, 2005). Great Britain and associated territories were the primary consumers of Belize's fisheries commodities prior to World War II (Thomspon, 1944); the United States thereafter (FAO, 1968; Shusterich, 1984). In parallel, fishery resource assessments in Belize started as expeditions in search of productive fisheries grounds overseas (e.g., Fiedler et al. 1943; Thompson, 1944).

Although Thompson (1944) described the fisheries of Belize in detail, the study focused on the northern region of the country, in the vicinity of Belize City (Fig. A.1.1), where the main fish and shelfish market then operated. Several limitations precluded direct quantification of catches in this report, leading to extrapolation of national landings from a restricted number of fishers that were interviewed during the study. The report documented how artisanal fishers targeted migratory shoals of "mutton" and "red" snapper in relatively "shallow" coastal regions around San Pedro (Fig. A.1.1) and during the rainy months of June-August (Thompson, 1944). "Red snapper" in the report referred to an aggregated fishery category constituted of "two or three species" of red color snapper. Harvested individuals were "quite large" and "fish of ten or twelve pounds [4.5-5.5 kg] were not uncommon" (Thompson, 1944). Although scientific names were not provided in the report, "mutton, red, and yellowtail snapper" were the dominant snapper fisheries in the report. This is the case in present time for Belize (Zeller et al.,

2011) and the rest of the GOH (Heyman and Granados-Dieseldorff, 2012), where mutton snapper is second to yellowtail snapper in finfish yields.

Before the 1950s, fishing in deep waters by fishers from the Placencia peninsula was extremely restricted, owing to the adverse meteorological and oceanographic conditions to which small sailing fishing vessels (or “Belizean smacks”) and paddling dugout canoes were exposed (Craig, 1966). Indeed, the vocabulary of Garifuna fishers from the area was “noticeably deficient in names of fish found in waters beyond the barrier reef” (Craig, 1966). Also, the catch needed to be sold alive at the dockside of the municipal market on Haulover Creek, Belize City, confining the ability of preserving the catch while fishers were offshore (Craig, 1966). Different to the commercial grouper fisheries that were already considered as overexploited at some locales (Craig, 1969), the mutton snapper fisheries of Belize were considered as largely underexploited (Thompson, 1944) or of subsistence (Craig, 1966). Around the 1950s, fishers from Placencia started venturing to catch snapper from the “abyssal waters”, where “the habitat of the richest fish resources lied”, particularly for “species of snapper that congregated on the successive, stair-like terraces to a depth approaching 200 meters” (Craig, 1966, citing Bradley, 1956).

Despite hurricane Hattie destroyed Seine Bight, Placencia, and much of the capital, Belize City, in 1961, fisheries production throughout the nation spurred creation of several fishing cooperatives in the 1960s, including the Placencia Cooperative, established in 1962 (Craig, 1966; Palacio, 1982; Key, 2002). The artisanal mutton snapper fishery at Gladden Spit might have become commercially oriented in the 1970s, after the Placencia Cooperative started generating electricity and producing ice in support of the productive conch and lobster fisheries (Table A.2.2 and Fig. A.1.5). Landings surged in the early 1980s, when motorized Mexican-style skiffs started to be introduced in Placencia peninsula (Key, 2002; Gray, 2009), replacing traditional dugout canoes and Belizean smacks.

Catch and effort estimates from the mutton snapper fishery at Gladden Spit fluctuated prior and after 1998, when the FSAs at Gladden Spit started to be monitored by The Nature Conservancy and the Belize Fisheries Department (Fig. A.1.5). Based on my reconstructed catches, the fishery endured a sharp decline in landings (76.4 % decrease) between the mid-1980s and the late 1990s (Fig. A.1.5). During this period, two important socioeconomic changes occurred simultaneously in Belize and likely contributed to this observed trend. In 1985, fishing cooperatives across the nation were impacted by the precipitous decline in the production and export of lobster and conch (King, 1997; Huitric, 2005). This led fishers from the Placencia peninsula and surrounding areas to reduce considerably their commodity contributions to the Placencia Cooperative and several of them forfeited their cooperative membership (Key, 2002). In the mid-1980s, tourism development began to expand rapidly in Belize (Key, 2002; Alexander, 2008; Gray, 2009). In the late 1980s, many fishers in the study area, a region with great tourism potential, left their fishing profession for jobs in the tourism industry, in search of more stable and predictable profits (Key, 2002; Key and Pillai, 2006). Between 1988 and 1998, the number of hotels in Placencia increased 390% (from 10 to 49 hotels) (Fig. A.1.5), while in the entire country, revenues from tourism quadrupled

(Key, 2002). In contrast, the maximum number of boats actively fishing at Gladden Spit on a daily basis dropped 79.2 % (from 72 to 15 boats) during the same period (Fig. A.1.5). Despite the marked differences in catch sizes between the periods of 1985-1991 and 1999-2011, the pattern was different when catches were standardized to CPUE, increasing slightly from 1.7 to 1.8 kg*hook-h^{-1} (5.9 % increase) between 1991 and 1999, and from 1.7 to 3.2 kg*hook-h^{-1} (88.2 % increase) between 1991 to 2011 (Fig. A.1.5).

2.3.2. Monitoring and management period of the fishery (1998-2011)

My quantitative analyses are based on 171 days of landings surveys conducted at Buttonwood Caye between 1999 and 2011 (Table A.2.1.). A total of 17,754 adult mutton snapper (49.0 t), caught during 626 boat-days fishing, were landed and surveyed (Tables A.2.1 and A.2.3). The maximum estimated number of boats landing on a single day was 10 and it was recorded in May 2011 (Table A.2.3). Most of the sampling effort was allocated in May (40.3 % of the total 171 days surveyed between 1999 and 2011) (Table A.2.1). Inconsistent sampling in the other months (March, April, and June) and the frequent replacement of landings teams (as recorded in database) leaded to deviations from the expected power model ($W = a*L^b$, W is fish weight, L fish length, and a and b growth constants) in annual length-weight relationships for landed mutton snapper (Fig. A.1.6). May landings accounted for 64.5 % of the total number of individuals landed between 1999 and 2011 and 63.9 % of the corresponding total weight (Table A.2.3). From 1999 to 2011, sex ratios (M:F) averaged 1.2:1 with little variation (Table A.2.3).

Most of the sampling effort (69.9 %) for landings was concentrated between 2006 and 2011 (Table A.2.1). The maximum annual sampling effort was completed for this study in 2011, with a total of 47 days surveyed. Only year 2011 was surveyed during the entire fishing season (March-June). To account for uneven sampling effort and data availability and following my study design, the remainder of the results in this chapter is based on estimates derived from May data only.

The inter-annual trends in both landings and fishing effort fluctuated between 1999 and 2011 (Table A.2.3; Figs. A.1.5 and A.1.7). A similar fluctuation pattern was exhibited by UVC-Abundance, with particular proportionality between 2006 and 2011 (Table A.2.3 and Fig. A.1.7). Two discernible phases, 1999-2006 and 2007-2011, were captured by analyses. The break-point (2006) coincides with two socio-environmental events (Table A.2.2): 1) the issuing of "special licenses" in favor of restricting mutton snapper fishing at Gladden Spit to patriarch fishers and 2) the increase in presence and enforcement in the area by the co-managers of GSSCMR.

CPUE-Abundance declined significantly between 2001 and 2003 but recovered thereafter (posterior PERMANOVA pair-wise tests: $p \leq 0.005$) (Fig. A.1.8A). CPUE-Abundance in 2011 was significantly higher (posterior PERMANOVA pair-wise tests: $p \leq 0.04$) than in 1999, 2003, 2006, and 2007 (posterior PERMANOVA pair-wise test: $p = 0.76$). Similarly, CPUE-Weight declined significantly between 2001 and 2003, but recovered between 2003 and 2004 (posterior PERMANOVA pair-wise tests: $p \leq 0.005$) (Fig. A.1.8B). CPUE-Weight in 2011 was significantly higher than in 1999, 2003, and 2007 (posterior PERMANOVA pair-wise tests: $p \leq 0.03$).

The largest mutton snapper recorded from landings was a male, 905 mm TL and 11.8 kg, caught in May 2011 (Figs. A.1.9 and A.1.10A). The heaviest mutton snapper was also a male of 13.2 kg and 890 mm TL caught in May 2001 (Fig. A.1.10 B). Individual median lengths ranged from 490 mm TL (2008) to 570 mm TL (2001) (Fig. A.1.10 A). Individual median weights ranged from 2.72 kg (2004) to 3.63 kg (2001) (Fig. A.1.10 B). The most frequent size-at-capture classes also fluctuated between 1999 and 2011, ranging from 500 to 600 mm TL (Fig. A.1.9). No significant changes were detected in individual median lengths or median weights among years (one-way PERMANOVAs: pseudo-F ≤ 1.9, df = 9 and 59, $p \geq 0.10$).

2.4. Discussion

This chapter illustrates the history of the mutton snapper fishery at Gladden Spit in relation to key environmental and socioeconomic factors. After undergoing subsistence use prior to the 1960s (Craig, 1966), the fishery became more commercially oriented in the 1970s, when the Placencia Fishing Cooperative started generating electricity and producing ice that allowed better preservation of catches (Key, 2002). Mutton snapper landings probably surged in the early 1980s with the introduction of motorized Mexican-style skiffs to the Placencia Peninsula (Gray, 2009). Despite limitations in quantitative historical fishery data, I was able to reconstruct catches retrospectively and to capture a time, 24 years back, when fishing effort and the fishery yields were higher than recent times. The decrease in historical catches for the late 1980s and early 1990s are consistent with the findings of Graham et al. (2008) who used information from interviews with fishers. However, the interpretation of the declining trend is not simple and cannot be explained as a sole result of overexploitation since it occurred simultaneously with a decline in fishing effort and a shift in occupations and livelihoods of many fishers during the rapid development of the tourism industry in the area, described in the results. My analyses for the years between 1999 and 2011 show relatively stable CPUE estimates, proportionality between CPUE and UVC abundances, sustained values of individual sizes that are also concordant with the biological variables of the species (see Allen, 1985; Claro and Lindeman, 2004; Froese and Pauly, 2012), and continued preservation of M:F sex ratios. These data all suggest persistence of the fishery over this time period. Graham et al. (2008) also analyzed CPUE changes between 2000 and 2002, and concluded that the fishery was in decline. Nevertheless, as more years of data were available to me, I found that the only significant decline in the whole decade was between 2001 and 2003 and that the fishery did not continue on a declining trend. Moreover, the low CPUE detected in 2003 coincided with the low fishing effort and low catches recorded for that year. This drop in CPUE occurred the year after Hurricane Iris hit the area. Hurricane Iris was a Category-4 tropical storm (Saffir-Simpson Hurricane Scale) that made landfall in October 2001, exactly between Monkey River and Placencia (see Avila, 2001). The aftermath of Iris was one of the most severe in the hurricane history of the area and it took considerable time to the fishing villages that were devastated to recover and rebuild (Alexander, 2008; Gray, 2009).

Persistent mutton snapper fisheries have been documented in Cuba and the southeastern United States (Claro et al., 2001; Claro and Lindeman, 2003; SEDAR, 2008;

Claro et al., 2009). Individual fisheries show a range of resilience to fishing pressure, depending on various factors that include the intensity and nature of the fishing activity, the biology and life-history strategies of the species, the oceanography and meteorology of the fishing grounds, and the effectiveness of fisheries management (Pauly et al., 1996; Ault et al., 1998; Claro et al., 2009). In contrast to other reef fish, mutton snapper are eurytopic fish that tolerate wide ranges of environmental conditions throughout their ontogenetic development (Allen, 1985; Watanabe, 2001; Claro and Lindeman, 2004). Among the most important factors explaining the persistence of the mutton snapper fishery in Cuba were their advantageous life-history strategies (Claro et al., 2009). Compared to other snappers and groupers of Cuba, mutton snapper use a large number of spawning sites (Claro, 1981; García-Cagide et al., 2001; Claro and Lindeman, 2003) and the species aggregates to spawn in relatively deep waters (Claro and Lindeman, 2004; Claro et al., 2009). Further, large feeding areas are often located close to spawning sites (Claro et al., 2009). Cuban mutton snapper fisheries also persist since they are targeted with hand lines, a more selective and less destructive fishing gear than seines, set nets, and bottom trawls used for other species. Since all the factors favoring the persistence of mutton snapper fisheries in Cuba are present in my study area, I can only hypothesize that they also play a role in the persistence of the fishery at Gladden Spit. Fishers have traditionally used hand lines at the site, which are considered the least destructive fishing gear across the Caribbean (Munro, 1983). Gladden Spit is one of the other four protected sites (Caye Bokel, Glover’s Long Caye, Seal Caye, and Rise and Fall Bank; Fig. A.1.2) where mutton snapper aggregate to spawn along the Belize Reef (Heyman and Requena, 2002; Kobara and Heyman, 2010). Furthermore, fishing in these other four sites is presently banned throughout the year, as they are managed as permanent No-Take Zones (Government of Belize, 2003b). At Gladden Spit, fishing is banned outside of the season (March-June). Finally, mutton snapper aggregate to spawn at Gladden Spit between March and September every year and similar to their conspecific snappers from Cuba, mutton snapper also spawn in relatively deeper waters than the other species that also use the site (Heyman and Kjerfve, 2008).

It is generally agreed that reef fish spawning aggregation fisheries are likely to be sustainable only at limited, subsistence harvest levels (Sadovy and Domeier, 2005; Sadovy De Mitcheson et al., 2008). Only a stock assessment of the mutton snapper fishery at Gladden Spit, that includes estimation of age-specific mortality rates and growth parameters, could project effective sustainable harvest levels. It is also important to mention that, since the relationship between a fishery's CPUE and its population size is non-linear and disproportional (Beverton and Holt, 1957; Hilborn and Walters, 1992; Arreguín-Sanchez, 1996), the evaluation of fishery status using catch-based data such as the variables estimated for this study, should always be interpreted with caution. The most commonly assumed situation of disproportionality for aggregating fisheries is when estimates of CPUE can remain high even if the abundance of the exploited stock declines, a situation known as "hyperstability" (Hilborn and Walters, 1992). Although empirical support is still needed, tropical reef fish spawning aggregation fisheries are considered to exhibit hyperstability because of the highly dense fish concentrations that recurrently yield high catches in relatively short amounts of time at specific sites (Monroy-García et al., 1996; Sadovy and Domeier, 2005; Erisman et al., 2011; Russell et al., 2012).

Many marine fish stocks consist of amalgamations of components from several geographic locations (Beddington and May, 1977; Hilborn et al., 2003; Beddington et al., 2007). I consider catch and abundance of mutton snapper estimated in this study to be a sample from a larger putative mutton snapper stock from which the fishery has been taken. Despite the need for further research, the mutton snapper stock from which the fishery at Gladden Spit is extracted could include individuals migrating for reproduction from a broader geographic area (i.e., the catchment area of the mutton snapper FSA, *sensu* Zeller, 1998) that expands beyond the limits of GSSCMR and perhaps Belize. Mutton snapper is a highly migratory species (Beaumariage, 1969; Claro and Lindeman, 2004), with a high degree of population connectivity in the western Caribbean inferred from biophysical modeling (Paris et al., 2005) and genetic tracers (Shulzitski et al., 2009; Carson et al., 2011). Fishers, tourism guides, and other stakeholders indicated that migratory shoals of mutton snapper, presumably migrating from the western Bay Islands in Honduras where these shoals are a major artisanal fishery (Gobert et al., 2005), are known to precede the dry season and have been recurrently spotted around the southern Belize Reef. They also reported the recurrent migratory shoals of “small-size” mutton snapper (juvenile individuals, presumably) entering the estuarine Placencia Lagoon with the arrival of the first frontal winds, a pattern also noted by Thompson (1944) and Craig (1966) for mutton and other snapper species at other coastal estuarine regions from northern Belize. Neither these migratory pathways, nor the other four known mutton snapper FSA sites were accounted by this study. By ignoring mutton snapper abundances from unfished sites (e.g., its other four FSA sites and other habitats from its broader putative catchment area), and assuming that they behave the same as the fished sites in accounts of abundance, one can underestimate the fishery's population size (Walters, 2003).

Fishery regulations established with the declaration of GSSCMR effectively closed the multi-species spawning aggregation to fishing except for allowing fishers to fish the spawning aggregation only from March through June every year and only during daylight hours. While allowing fishing for mutton snapper, therefore, the regulations provided protection for other snapper species, such as cubera snapper that typically spawn around sunset (Heyman et al., 2005) and groupers, such as Nassau grouper (*Epinephelus striatus*, family Epinephelidae), that spawn between December and March at Gladden Spit (see Heyman and Kjerfve, 2008). Management measures aimed at directly limiting the number of fishers at Gladden Spit during spawning season were established in 2003 (Government of Belize, 2003a, b), and implemented in the field in 2006. The measure consisted of issuing "special licenses" only to traditional fishers but the legal definition is still vague and no maximum number of access licenses has been established. Nonetheless, enforcement increased after 2006 when co-managers had more resources available for patrols and monitoring of the reserve's spawning aggregations, including landings surveys and underwater visual censuses. My data showed an increase in fishing effort and landings after 2007. Faced with the limitations for projecting sustainable harvest rates, and in the best interest of the fishery and its management objectives, it is imperative that the granting process of special licenses be reviewed and updated and that intensive data collection and analysis be continued to closely monitor the fishery and guide management.

I consider that the current co-management structure of GSSCMR presents assets for successful fisheries management and the persistence of the mutton snapper fishery at Gladden Spit, so long as strong fishers' involvement, stakeholder representation, and the cooperation and support from local governments and fishery and conservation policy makers are maintained. The platform exists for cooperation among co-managers, fishers, and rest of stakeholders in resource monitoring, evaluation, and decision making. Fishers, community leaders, and other stakeholders have representation in the advisory committee that develops the regulations for GSSCMR (see Government of Belize, 2003a) and these are regularly discussed during participatory consultations held at local communities throughout the year. Indeed, fishers played an important role in lobbying for the declaration of GSSCMR (Heyman and Graham, 2000; Heyman, 2011) and even before its declaration, fishers have continuously and actively participated in the landings surveys of the mutton snapper fishery. Stakeholder-centered approaches to marine resources conservation and management, with strong local leadership, effective self-enforcement by local stakeholders, and empowerment from the broader community can be more successful than reserves with top-down mandated preservation (Aburto-Orepeza et al., 2011; Berkes, 2012; Cinner et al., 2012; Costello et al., 2012). This approach is considered key in the management of reef fish spawning aggregations (Russell et al., 2012) and the most viable in rural settings where the food and economic securities of people rely directly on local natural resources (Gutierrez et al., 2011; Frédou et al., 2009b), such as within the Gulf of Honduras and Belize (Heyman and Granados-Dieseldorff, 2012).

2.2.5. Summary

Several artisanal fisheries across the Caribbean have historically targeted recurrent and massive fish spawning aggregations (FSA) of valuable snappers. Artisanal fishers have harvested mutton snapper (*Lutjanus analis*) from the Gladden Spit FSA site in Belize since the 1950s, with catches contributing considerably to the national finfish yields for decades. The Government of Belize partnered with stakeholders from southern Belize to co-manage the area, declaring a multi-use marine reserve at Gladden Spit in 2000. The overall objective of this chapter was to holistically evaluate the status of the fishery with intensive involvement of stakeholders, by re-constructing the environmental and socioeconomic history of the fishery (1950-2011), including evaluation of all existing quantitative fishery data (1991-2010) and intensive collaborative new data collection during 2011. Analyses show that catch per unit effort, individual sizes, and sex ratios have been relatively stable throughout the fishery's history, with a sharp reduction in total landings and fishing effort in the 1980s, parallel to a rapid growth in the tourism industry. Although annual landings have fluctuated over time, this FSA fishery has persisted for over 60 years and landings are highly dependent on external socio-environmental factors. The life-history strategies of mutton snapper are distinct from most vulnerable FSA fishes and confer the species more resistance to natural and anthropogenic stressors, including

fishing. Key to successful long-term, adaptive co-management of the fishery is a continued involvement of fishers and other stakeholders in resource monitoring and evaluation, as well as in policy and decision making.

CHAPTER III

WITHIN-SEASON DYNAMICS OF THE MUTTON SNAPPER (*Lutjanus analis*) SPAWNING AGGREGATION FISHERY AT GLADDEN SPIT, BELIZE

3.1. Introduction

Throughout the Caribbean and the subtropical waters of the Western Atlantic, mutton snapper (*Lutjanus analis* Cuvier 1828, family Lutjanidae) is a valuable, commercially-harvested reef fish species (Claro, 1981; Allen, 1985; Claro and Lindeman, 2004). Despite their increasing market demand as excellent food fish, the status of their fisheries has been sparsely assessed (e.g., Claro and Lindeman, 2004; SEDAR 2007, 2008; Frédou et al., 2009a, b) and their management continues to be largely disregarded. Moreover, the species is considered to be vulnerable to extinction (Huntsman, 1996), a condition that threatens the sustainability of its fisheries and those who depend on them. Uncontrolled harvest of mutton snapper at their highly predictable and dense spawning aggregations is considered an important factor that contributes to their vulnerability (Domeier and Colin, 1997; Burton, 2002; Claro and Lindeman, 2003).

During their life cycle, mutton snapper share similar habitats with several other snapper species and are usually targeted as multi-species reef fishery complexes of peculiar productivity, location, and seasonality (Claro and Lindeman, 2003; Frédou et al., 2006; Heyman and Granados-Dieseldorff, 2012). Juveniles inhabit inland estuaries, mangroves, and seagrass beds, while adults inhabit coral reefs, and migrate to spawn in aggregations (Claro, 1981; Allen, 1985; Claro and Lindeman, 2004). Faced with the fragility of fish spawning aggregations and their importance for sustaining yields from several commercial species, the Government of Belize protected 11 of the nation's multi-species spawning aggregation sites along the Barrier Reef and declared them in 2003 as non-extractive zones (NTZ), seasonally or permanently closed to fishing (Government of Belize, 2003a, b; Heyman, 2011). Mutton snapper aggregate to spawn in four of these NTZ (Caye Bokel, Gladden Spit, Seal Caye, and Rise and Fall Bank), in addition to Long Caye that is within the multi-use Glover's Reef Marine Reserve (Heyman and Kjerfve, 2008; Kobara and Heyman, 2010).

Since the 1950s, artisanal fishers have targeted mutton snapper during their peak spawning aggregation season (March-June) at Gladden Spit (Chapter II). Gladden Spit is a reef promontory located 40 km east of the coastal village of Placencia (Fig. A.1.2) and that hosts multi-species spawning aggregations (Heyman and Kjerfve, 2008). The site lies within a 16.2 km^2 NTZ in the northeastern portion of Gladden Spit and Silk Cayes Marine Reserve (GSSCMR), a multi-use reserve of ~105.2 km^2 declared by the Government of Belize in 2000 (Government of Belize, 2000; Government of Belize, 2003a, b). The marine reserve is currently co-managed by the Belize Fisheries Department (BFD) and the Southern Environmental Association (SEA), a community-based nongovernment organization based in Placencia (Chapter II).

Previous studies on mutton snapper at Gladden Spit have described inter-annual trends of the fishery landings at Buttonwood Caye, the main landing site for mutton snapper from the area (Heyman and Graham, 2000; Graham et al., 2008; Chapter II), and the courtship and spawning behavior of individuals during spawning aggregations

(Heyman and Kjerfve, 2008). However, the size, age structure, and degree of maturation of the reproductive individuals throughout the spawning season have not been described. Size, age, and maturity of adult marine fishes are fundamental determinants for assessing responses of their populations to fishing pressure and environmental stresses (Ricker, 1954; Trippel, 1995; Berkeley et al., 2004). Moreover, little is known on the co-occurrence and interactions of the mutton snapper fishery with other nontarget fish species at Gladden Spit. The incidental capture of these nontarget species, commonly known as bycatch and characteristic of highly biodiverse Caribbean fisheries (Medley et al., 1993; Pauly et al., 1996), impacts not only the ecological community, but also the yields of target species (Alverson and Hughes, 1996; Hall, 1996; Crowder and Murawski, 1998).

Given that fishers have traditionally targeted the mutton snapper spawning aggregation at Gladden Spit during the peak of their reproduction period, it is possible to use their landings at Buttonwood to assess the size and age structure of reproductive mutton snapper, their degree of maturation, and interactions with co-occurring bycatch species. In this chapter I describe the within-season dynamics of the mutton snapper spawning aggregation fishery at Gladden Spit from March to June 2011 and present basic biological and fisheries data that may contribute to the creation of specific management and conservation strategies. Specifically, I aimed to 1) characterize the within-season fishing and landings dynamics of the mutton snapper fishery at Gladden Spit and its associated bycatch using fishing-fleet and catch-based data; 2) characterize the size and age structure, as well as the degree of maturation, of reproductive individuals through otolith and gonad analyses; 3) test whether individual size, age and degree of maturation vary in relation to the lunar cycle and among months of the peak spawning season; and 4) test whether the fishing fleet and bycatch species composition change among months.

3.2. Material and methods

3.2.1. Study area and fishery

Along the Belize Barrier Reef, Gladden Spit (16.5° N 88.0° W) is one of the prime sites that hosts multi-species fish spawning aggregations (Fig. A.1.2). Among the 21 species that aggregate to spawn at Gladden Spit, mutton snapper is prominent in biomass (Heyman and Kjerfve, 2008). Mutton snapper spawning aggregations at the site span from March to September every year and peak three-eight days after full moon (dafm) in March-June, with the actual spawning activity restricted mainly to 13:00-15:00 h (Heyman and Kjerfve, 2008).

During most of the year, fishing is prohibited at Gladden Spit (Government of Belize, 2003a, b). The only exception is when the site opens for limited traditional harvest of mutton snapper, 10-14 days around the full moons of March-June. Fishing is allowed only during daylight hours (6:00-17:00 h) and it is regulated through "special licenses" issued by the co-managers of GSSCMR to a limited number of artisanal fishers (Government of Belize, 2003 b), a norm that has been difficult to enforce and that is still in negotiation (Graham et al., 2008; Heyman, 2011; Chapter II).

Using hand lines, fishers from the coastal villages of Hopkins, Seine Bight, Placencia, Independence, and Monkey River (Fig. A.1.2) have traditionally targeted the mutton snapper spawning aggregations found at 20-60 m depths on the forereef region of Gladden Spit (Chapter II). Buttonwood Caye (Figs. A.1.2 - A.1.4) has traditionally been the primary base camp and landing site for mutton snapper from Gladden Spit and the Placencia Producers Cooperative Society Ltd. (Placencia Cooperative, hereafter) the major buyer. The history and inter-annual dynamics of the artisanal mutton snapper at Gladden Spit are presented elsewhere (Chapter II).

3.2.2. Field sampling

Mutton snapper landings at Buttonwood Caye were sampled between March and June 2011. Following the design for landings surveys implemented by the co-managers of the fishery (BFD and SEA), monthly samplings lasted 10-13 days in total and started two-three days before the full moon (dbfm). For every boat landing at Buttonwood Caye, semi-structure interviews to fishers during landings surveys (see Chapter II) recorded the name of the captain, number of round trips from Buttonwood Caye to Gladden Spit (boat-fishing-trips; ~20 km roundtrip distance), total duration of fishing trips (±0.5 h soak time), number of fishers per boat (1-3 fishers, including the captain), fishers' village of residence, main selling market or cooperative, and fish marketable form (whole or fillet) and buying price (BZ$*kg^{-1}, with 2 BZ$ equivalent to 1 US$).

At the dockside, all fishes (mutton snapper and bycatch species) in boats were sorted and identified to the lowest possible taxon according to Smith (1997) and Humann and DeLoach (2002). Before fishers eviscerated their catch, all mutton snapper were measured for total length (TL, ±1 mm) and total weight (TW, ± 0.2 kg). Only the largest individuals from each bycatch species were measured and weighed. While fishers eviscerated their catch, the sex of each mutton snapper was recorded (female, male, undetermined), gonads weighed (GW, ± 0.1 g), and gonad state (i.e., reproductive development) macroscopically determined. Following García-Cagide et al. (2001), gonad state for males was recorded as Type I (early, immature, or resting: no whitish milt observed in testes) or Type II (late, mature, or sperm released: whitish milt evident in testes). Similarly, gonad state for females was recorded as Type I (early, immature, or resting: small, yellow pale ovaries, with no evidence of vascularization), Type II (late, developing, or mature: evidence of eggs in vascularized yellow ovaries of more intense color), Type III (running ripe, ovulation ongoing: evidence of transparent hydrated oocytes in inflated ovaries), or Type IV (spawned, or spent: flaccid ovaries, purple red).

Not all the boats fishing at Gladden Spit were sampled because some boats were missed when several boats landed simultaneously at the end of the day, some returned directly to mainland from Gladden Spit, or if fishers eviscerated their catch at sea before landing. Nevertheless, based on patrol reports from Park Rangers of the reserve, the total number of boats sampled for this study at Buttonwood Caye represented 76% of all the boats that were fishing at Gladden Spit. None of these limitations should affect sample representativeness or data analyses as presented.

3.2.3. Data analysis

Fishing effort was estimated by boat (boat-d-fishing) and by man hours fished (hook-h). The fishing fleet at Gladden Spit is constituted of Mexican-style skiffs with a maximum of three fishers on board (Chapter II). At the site, each fisher uses one baited hand line for harvesting mutton snapper for either a half or a full day (Chapter II). Considering this, I assumed that one boat-d-fishing was equivalent to either two boat-fishing-trips or more than eight h of soak time. Catch was estimated by numbers (fish) and by weight (kg) and then standardized to catch per unit effort (CPUE) as CPUE-Abundance (either fish*boat-d-fishing^{-1} or fish* hook-h^{-1}) and CPUE-Weight (either kg*boat-d-fishing^{-1} or kg*hook-h^{-1}) using the total-ratio method (Malvestuto, 1996). Though CPUE estimated by weight has traditionally been used in fisheries science, Pauly et al. (2013) recommend also estimating CPUE by abundance since changes in the total biomass of fish caught (i.e., CPUE-Weight) does not necessarily reflect changes in their harvested abundance.

For mutton snapper, female and male data were combined in size-based analyses as no significant differences in log-transformed TL and TW between sexes were detected *a priori*. Female to male (F:M) ratios were calculated in order to track sex proportions throughout the study period. For comparisons purposes with similar studies that used standard length (SL) or fork length (FL) of individual mutton snapper (sexes combined), the following equations from SEDAR (2008) were used in length transformations:

$$SL = -13.53 + 0.882 * FL \text{ and } TL = 8.804 + 1.087 * FL.$$

Total weight (TW) and gonads weight (GW) of mature male and female individuals were used to determine gonad development through estimations of individual gonadosomatic indexes (GSI) using the following relationship (García-Cagide et al., 2001):

$$GSI = (GW/(TW-GW)*100).$$

Gonad state (Type I-IV) and GSI were combined to evaluate degree of maturation of individual females and males based on macroscopic observations. Since gonad state was not confirmed through histological analysis and size and age of individuals in landings were restricted to those targeted by the fishery, data precluded statistical fitting of length and age at maturity. Considering these limitations, degree of maturation in this study was descriptively determined by considering only individuals with GSI>1.5 and gonad state Type II or beyond as mature (see Martínez-Andrade, 2003). This descriptive determination was based on that length (or age) at maturity is the smallest length category (or age class) in which >50% of the individuals of a given population are mature for the first time during the spawning season (Beverton and Holt, 1957).

For each bycatch species, the mean TL and TW of measured individuals were calculated in order to estimate bycatch biomass by species, month, and fishing season (March-June), and explore state of maturity. For the latter, the mean TL (mTL) of each species was compared to the mean length at first maturity (Lm) as reported for the species by Froese and Pauly (2012). Individuals were considered as immature if mTL < Lm. Raw species richness (%) of bycatch in monthly landings was estimated as the percentage of the number of bycatch species caught in a given month relative to the total bycatch species landed during the entire sampling period.

3.2.4. Otolith analysis

In the field, sagittal otoliths (sagittae) were removed from 115 randomly selected mutton snapper at Buttonwood Caye during landings surveys and after their TL, TW, sex, GW, and gonad state were recorded (see 3.2.2., previously). Combining the protocols of Mason and Manooch (1985) and Secor et al. (1991), sagittae were extracted at the dockside by making a cross-cut in the cranium of the fish with a hacksaw to maximize their exposure or, by opening the otic bulla with a wood chisel and entering the cranium from under the operculum, up through the gills. Sagittae were then rinsed with fresh water, wiped clean, and stored dry in labeled individual containers for transportation to the laboratory.

In the laboratory, left or right sagittae were randomly selected, measured (±0.1 mm) and weighed (±0.001 g). Based upon protocols described by Rooker et al. (2004), sagittae were then mounted in epoxy resin and sectioned along a transverse plane, adjacent to the core, using a low-speed Buehler Isomet saw. Thin sections (0.3-0.5 mm thick) were then attached to petrographic microscope slides with thermoplastic cement, polished to the core in sequence with 400-, 600-, 800-, and 1200-grit sandpaper, and ultimately polished with type A alumina powder (0.3 μm).

Annual age estimates were determined by counting the number of opaque growth increments from the core to the outer margin under a Zeiss Discovery V8 dissecting microscope with reflected light. Following Burton (2002), it was presumed that opaque increments were annuli, with age (years) equal to the number of increments counted.

Otoliths were read randomly twice and ages were assigned as the average of two counts for each otolith.

Growth parameters were estimated using the von Bertalanffy growth equation (VBGE) model. The VBGE is described as

$$L_t=L_\infty(1-e^{-k(t-to)}),$$

where L_t is TL (mm) at age t (years), L_∞ the mean asymptotic TL (i.e., the TL that a fish of a given population would reach if they would grow indefinitely), K the Brody growth coefficient (i.e., the rate per year at which the asymptotic length is approached), and t_o the initial condition parameter or time at hatch (Ricker, 1975). Following Haddon (2011), a nonlinear regression, using the least-squares method with the Solver Add-in in Microsoft Office Excel, was used to fit observed lengths at age to predicted ages by the VBGE. The VBGE that best fitted the observed data was then used to project ages of all individuals that were not aged with otolith-based techniques.

3.2.5. Statistical analysis

Data were arranged for statistical analysis following a two-factor balanced design and using days (d) as sample units for daily and monthly comparisons of fishery data (catch abundance and weight, fishing effort, CPUE-Abundance, CPUE-Weight, bycatch composition, fishing fleet composition,) and biological variables (individual mutton snapper TL, TW, GSI, and degree of maturation). Given that 1) sampling effort was unevenly distributed among months (n=13 days in March, n=9 days in April, n=10 days in May, n=10 days in June) and 2) the rhythmicity and synchronization of mutton snapper spawning aggregations follow the full moon cycle, two independent factors, days relative to full moon (drfm) and month, were selected for statistical analyses. Factor 1 (drfm) had nine fixed levels (-1 to 7 drfm), with -1 meaning 1 day before full moon, 0, the day of full moon, and positive numbers indicating days after full moon. Factor 2 (month) had three fixed levels (April, May, and June). (Note that March samples were excluded from analyses to avoid statistical noise since very few mutton snapper were landed that month (see section 3.3.1). Therefore, the total number of sampling units in the statistical design was 27 days.

Daily and monthly variations in the selected fishery and biological variables were analyzed by tests of permutational MANOVA and ANOVA (PERMANOVAs - Anderson, 2001a; McArdle and Anderson, 2001). Tests were run using the PERMANOVA+ package (Anderson et al., 2008) in PRIMER (Plymouth Routines In Multivariate Ecological Research) version 6 (Clarke and Gorley, 2006). Given the nature of the data in this study, PERMANOVAs were selected as more versatile and robust non-parametric alternatives to univariate and multivariate ANOVAs (Anderson, 2001b).

Univariate one-way PERMANOVAs were used to test for the separate effects of drfm and month on the fishery (catch abundance and weight, fishing effort, CPUE-Abundance, CPUE-Weight) and biological (mutton snapper TL, TW, and GSI) variables. Replication in tests was attained by analyzing each factor separately as follows: three monthly replicates in tests with drfm as the main effect and nine daily replicates in tests with month as the main effect. Data were log-transformed (log[x+1]) *a priori* and tests were based on Euclidean-distance matrices. Mean-squared errors, pseudo-F ratios (analogous to F-ratios in ANOVA), and p-values were obtained from 9,999 permutations (α=0.05). Posterior pair-wise tests of significant factors effect (drfm or month) were based on comparisons obtained also from 9,999 permutations (Anderson et al., 2008).

Multivariate one-way PERMANOVAs (Anderson, 2001a; McArdle and Anderson, 2001) tested monthly differences in the bycatch species composition and the fishing fleet boats composition. For each analysis (bycatch composition and fleet composition), a matrix of sampling days vs. either species (abundances) or boats (presence/absence) was built; month was set as the main effect. In order to reduce statistical noise from infrequent variable occurrences, only the most frequently landed species and landing boats were used in analyses. Data in matrices were fourth-root transformed and tests were based on Bray-Curtis similarities, given the large number of zeros from the data arrangement (Anderson et al., 2008). Analyses, mean-squared errors, pseudo-F ratios (analogous to multivariate Fs in MANOVA), posterior pair-wise testing, and p-values were obtained from 9,999 permutations (α=0.05).

To visualize the multivariate pattern among daily observations of bycatch and fishing fleet composition, non-metric multidimensional scaling (NMDS) was performed on Bray-Curtis distances (Kruskal and Wish, 1978) in PRIMER 6 (Clarke and Gorley, 2006). NMDS were based on presence-absence matrices of either boats or species (with a value of 0 denoting absence and a value of 1, presence) by sampling day. In ordination plots, NMDS scores were ordered by month (March-June). For each NMDS, the number of iterations was set to 50 and the minimum stress in Kruskal fit schemes to 0.01. Following Clarke and Warwick (2001), group contours were then graphically traced by superimposing group-averaged clusters from Bray-Curtis similarities to 2-dimensional NMDS graphical configurations, at similarities of 50%.

The degree of maturation of landed individuals was analyzed following an unreplicated randomized block design in two-way multivariate PERMANOVAs (Anderson et al., 2008). The daily catch composition in females and males at a given gonad state was used as an indicator of the degree of maturation of the reproductive individuals in spawning aggregations. Female and male data were analyzed separately in PERMANOVAs and either drfm or month was used as the block factor in analyses. Daily sex-specific abundances were arranged *a priori* in a matrix of sampling days vs. gonad state (Type I-IV for females, Type I-II for males). Abundances were fourth-root transformed and tests were based on Bray-Curtis similarity matrices. Due to the lack of replication of the two-way design, it was assumed that the highest-order interaction term in multivariate tests was zero (Anderson et al., 2008). Analyses, mean-squared errors, pseudo-F ratios, posterior pair-wise testing, and p-values were also obtained from 9,999 permutations (α=0.05).

3.3. Results

3.3.1. Within-season fishing and catch dynamics

Between March and June 2011, a total of 23,756 fish from 50 species, amounting to 28.9 t, were caught during 168 boat-d-fishing at Gladden Spit and landed at Buttonwood Caye (Tables A.2.4 and A.2.5). By numerical abundance, mutton snapper represented 21.2% of the total landings (5,047 mutton snapper), by weight, 42.6% of the total landings (12.3 t).

Fishing effort fluctuated in relation to the full moon cycle and throughout the fishing season (Table A.2.4 and Fig. A.1.11A). Fishing effort was significantly highest in May (41.5 % of the total 3,183 hook-h fished during the sampling period), followed by March (25.8 %), June (16.4 %), and April (16.3 %) (one-way PERMANOVA: pseudo-F=12.94, df=2 and 24, p=0.0003). The fishing fleet varied significantly in composition throughout the season (one-way PERMANOVA: pseudo-F=12.75, df=3 and 26, p=0.0001), with significantly distinct fishing fleets among months (posterior-PERMANOVA pair-wise tests: p<0.010) and as depicted by discernible groups of boats in NMDS plots (Fig. A.1.12). Not all boats fished all days in a given month and not all boats fished continuously throughout the season. Most of the fishing boats were from the village of Placencia (16 boats), followed in numerical abundance by Independence (8 boats), and Monkey River (3 boats).

Daily landings of mutton snapper fluctuated in relation to the full moon cycle and varied among months (Table A.2.5; Figs. A.1.11B and A.1.11C). Abundance of mutton snapper in landings was significantly highest in May (51.2% of the total 5,047 mutton snapper landed during the sampling period), followed by June (40.4%), April (8.2%), and March (0.2%) (one-way PERMANOVA: pseudo-F=12.8, df=2 and 24, p=0.0002). Males were slightly more abundant than females, with F:M sex ratios maintained at 1:1.3 between March and June. By weight, mutton snapper landings were also significantly highest in May (57.6% of the total 12.3 t landed), followed by June (31.7%), April

(10.5%), and March (0.2%) (one-way PERMANOVA: pseudo-F=9.5, df=2 and 24, p=0.0001).

Monthly mutton snapper CPUEs (CPUE-Abundance and CPUE-Weight) increased progressively with the ongoing fishing season (Table A.2.4; Figs. A.1.11D and A.1.11E). March data were excluded from further analyses because CPUEs were minimal in that month. CPUEs peaked on 3-5 drfm in April, 3-4 drfm in May, and 2-4 drfm in June. No significant differences were detected in CPUEs among drfm (one-way PERMANOVAs: pseudo-F<0.44, df=8 and 18, p>0.88). CPUEs did vary among month (one-way PERMANOVAs: pseudo-F>17.0, df=2 and 24, p<0.0002), with CPUEs highest in June and followed by May and April, respectively.

Bycatch abundance and species composition in daily landings varied throughout the fishing season (Table A.2.5) and as depicted by the different NMDS clusters observed in Fig. A.1.13. Abundance of bycatch individuals was highest in March (93.1% of the total 18,709 individuals landed), followed by April (3.5%), June (2.6%), and May (0.8%) (Table A.2.5). The species composition of bycatch varied among months (one-way PERMANOVA: pseudo-F=9.52, df=3 and 36, p=0.0001), with no significant differences detected between April and May (posterior-PERMANOVA pair-wise tests: p=0.18). The bycatch composition was more diverse in March (69.4% of all the 49 species landed between March and June), followed by April (55.1%), June (42.9%), and May (38.8%). Fourteen of the bycatch species are known to form spawning aggregations and four of them, yellowtail snapper (*Ocyurus chrysurus*, family Lutjanidae), red hind (*Epinephelus guttatus*, family Epinephelidae), dog snapper (*Lutjanus jocu*, family Lutjanidae), and cubera snapper (*Lutjanus cyanopterus*, family Lutjanidae) were among the 15 most abundant bycatch species landed at Buttonwood Caye (Table A.2.5). Yellowtail snapper alone represented 86.4 % of the bycatch by numerical abundance (n=16,008) and 78.7% by weight (13.0 t). With the exception of red hind, all individuals in bycatch had mean TL>Lm.

Based on fishers' responses to semi-structured interviews, the main buyers for mutton snapper and bycatch products were Placencia Cooperative, Aquamar Shrimp Farms, and the Jamaica-based company Rainforest Seafoods, a major international corporation (Peteru et al., 2010). Not all the species in catches were marketable, especially those with reputation for ciguatera poisoning (Table A.2.5). Eviscerated mutton snapper and bycatch fish were sold as fresh and whole, with pre-set prices of US\$3.85*kg^{-1} for mutton snapper, US\$2.20*kg^{-1} for other snappers and groupers, and US\$1.10*kg^{-1} for the rest of the marketable bycatch species. The estimated total gross sales from the 2011 landings at Buttonwood Caye was US\$78,454, with US\$47,514 from mutton snapper (60.6% of the total gross profits), US\$28,174 from yellowtail snapper (35.9%), and US\$2,765 from the rest of marketable species (3.5%).

3.3.2. Size and age structure of reproductive mutton snapper

Individual mutton snapper sizes decreased significantly (one-way PERMANOVAs: pseudo-F>14.1, df=2 and 24, p<0.0001) with the ongoing spawning season, with both TL and TW smaller in June (posterior-PERMANOVA pair-wise tests: p<0.007) (Table A.2.4; Figs. A.1.14 and A.1.15). No significant differences were detected in individual sizes (TL or TW) among drfm (one-way PERMANOVAs: pseudo-F<0.95, df=8 and 18, p>0.50). In decreasing order, the most frequently caught size classes were 600-650 mm TL in April, 500-550 mm TL in May, and 450-500 mm TL in June (Fig. A.1.14). The largest mutton snapper landed was a male of 905 mm TL and 11.8 kg TW caught in May; the smallest individual landed was a male of 315 mm TL and 0.5 kg TW caught in June.

Age of mutton snapper, determined using otolith-based techniques (n=115), ranged from 2 to 16 years, with corresponding observed lengths of 310 and 830 mm TL, respectively (Fig. A.1.16). The VBGE that best fitted the data was $L_t=905.95*(1-e^{-0.13(t-(-2.04))})$ ($R^2=0.82$, $MSE=1.79*10^{-3}$, n=115). Based on this equation, the projected ages of all the mutton snapper measured in landings ranged between 2 and 50 years (limitations of age projections are discussed later in this chapter). After grouping individuals by age (year classes), most individuals (86.0% of the total individuals landed between April and June) were between age 3 and 7. Age-4 individuals were landed most frequently (31.4 %), followed by individuals in age 5 (19.6 %), age 3 (14.3 %), age 6 (12.4 %), and age 7 (8.3 %) (Fig. A.1.17A). Ages of individuals landed did not vary significantly among drfm (one-way PERMANOVA: pseudo-F=0.97, df=8 and 18, p=0.48), but did vary among month (one-way PERMANOVAs: pseudo-F=11.4, df=8 and 18, p=0.0005), with individuals significantly younger in June (posterior-PERMANOVA pair-wise tests: p<0.0003). In April, most mutton snapper were age 4 (20.0%), followed by age 5 (19.0%), and age 6 (17.1%). In May, the pattern was similar, with most mutton snapper in age 4 (29.2%), followed by age 5 (19.8%), and age 6 (13.5%). In June, the pattern was different, with most mutton snapper in age 4 (36.2%), followed by age 3 (24.8%), and age 5 (19.5%) (Fig. A.1.17B).

3.3.3. Degree of maturation of reproductive mutton snapper

Between April and June, 51.9% of the landed females were macroscopically determined to be sexually mature (i.e., individual GSI>1.5, gonad state Type II or beyond), with 22.4% in Type II gonad state, 29.3% in Type III, and 0.2% in Type IV (Table A.2.4; Fig. A.1.18). Most females (>50 %) were mature at age 4 and 520 mm TL. Conversely, 88.4% of the landed males were mature (Type II), with >50% mature at 4 years and 490 mm TL. The smallest mature female in landings was 380 mm TL (age 2, caught in May); the smallest mature male was 330 mm TL (age 2, caught in April).

Significant differences in female GSIs were detected only among months (one-way PERMANOVA: pseudo-F=4.61, df=2 and 24, p=0.01), with GSI values significantly smaller in June (posterior-PERMANOVA pair-wise tests: p<0.05). Female gonad states varied among month and among drfm (two-way PERMANOVA: pseudo-Fs>1.59, df=8, 2 and 16, p<0.04), with mature females peaking in abundance 3-7 drfm in April and -1 and 2-7 drfm in May. In June, 66.4 % of females were immature (Table A.2.4; Fig. A.1.18).

No significant differences were detected in male GSIs among drfm or among months (one-way PERMANOVAs: pseudo-F<0.86, df=8 and 18, p>0.59) (Table A.2.4). Male gonad states varied only among month (two-way PERMANOVA: pseudo-F=3.36, df=2 and 16, p=0.0001), with mature males significantly predominant in April (posterior-PERMANOVA pair-wise tests: p<0.01).

3.4. Discussion

3.4.1. Within-season fishing dynamics

The variability of CPUE in marine fisheries is affected by the biology and behavior of the target species, the target species' interactions with co-occurring taxa at fishing grounds, and by fisher's motivation and skills (Cooke and Beddington, 1984; Arreguín-Sánchez, 1996; Ward, 2008). In 2011 and consistent with prior years (Chapter II), fishing effort, catches, and the corresponding CPUE estimates (CPUE-Abundance and CPUE-Weight) of the mutton snapper fishery fluctuated around the days of full moon and differed significantly among months. In addition to the relative availability of aggregating mutton snapper at Gladden Spit, the temporal trends in CPUE resulted from the daily and monthly variations in fishing effort and catch efficiency from different fleets that operated at Gladden Spit every month.

Fishers at Gladden Spit allocate their fishing effort based on their knowledge of the lunar and seasonal dynamics of the aggregating fishes, in order to maximize their catch efficiency, as has been described for skilled fishers who follow their expert knowledge to anticipate when and where target species will be abundant (Beverton and Holt, 1957; Cooke and Beddington, 1984; Hilborn, 2007). Consistent with the historical pattern of the fishery, fishing effort and landings were highest in May, the most productive month for mutton snapper at Gladden Spit (Chapter II). The fishing activity was reduced in April, as most fishers returned to their home villages for Easter festivities, and in June, when fishers switched intermittently to the highly lucrative lobster (*Panulirus argus*, Palinuridae) fishery that opened on June 15. Typically, if March has an early full moon like it did in 2011, mutton snapper are not angled and fishing effort tends to be low. Nevertheless, in 2011, fishers targeted yellowtail snapper and therefore allocated a relatively high fishing effort in March, second to May in magnitude.

The composition of fishing fleets varied significantly among months as did fishers' skills and motivation. Boats did not fish all days in a given month nor all months in the fishing season. All fishers who targeted mutton and yellowtail snapper in this study used hand lines from vessels of similar size and engine power. However, there was ample variation in their skills and experience, which ranged from 2 to > 50 years. Older, more skilled fishers were unevenly distributed among boats. In terms of fishing motivation, most fishers had alternate occupations to fishing (e.g., agriculture, masonry, elementary teaching, hospitality, and tourism-related activities), as it has been previously reported (Heyman and Graham, 2000; Graham et al., 2008). Therefore, most fishers had other sources of income to offset days of no fishing.

3.4.2. Within-season catch composition

Between March and June 2011, mutton snapper constituted only 21.2% of landings at Buttonwood Caye in numerical abundance, 42.6% in biomass, and 60.6% in total profits. If one considers that bycatch is "the catch that is either used or unmanaged" (Davies et al., 2009), then mutton snapper was outweighed by bycatch in 2011, particularly by yellowtail snapper. Yellowtail snapper was particularly predominant in March landings and represented 67.4% of the total landings in numerical abundance, 44.3% in biomass, and 35.9% in total gross profits. Unfortunately, no published detailed bycatch data exist from landing surveys at Buttonwood Caye. Historically, yellowtail snapper has commonly been associated with mutton snapper in multi-species finfish fisheries in Belize (Thompson, 1944; Zeller et al., 2011; Heyman and Granados-Dieseldorff, 2012) and rest of the Western Atlantic (Claro 1981, 1983; Lindeman et al., 2000; Costa et al., 2003; Frédou et al. 2009a).

The catch and bycatch composition varied among the months surveyed. A total of 14 bycatch species are known to form spawning aggregations, including yellowtail snapper, the species that may be more heavily impacted. Yellowtail snapper (16,008 individuals landed in this study) aggregate to spawn at Gladden Spit between February and March every year (Heyman and Kjerfve, 2008), so a considerable period of the peak their spawning aggregations was unmanaged in 2011. The other 13 bycatch species known to aggregate to spawn at the site (see Table A.2.5) amounted to only 316 individuals (1.7% total 18,709 bycatch fish landed) and either individuals were immature (e.g., red hind) or adults aggregate to spawn nearby at other times of the day in March-June (e.g., dog and cubera snapper are dusk spawners) or off season (e.g., groupers aggregate that spawn during colder months at Gladden Spit) (see Heyman, 2001; Heyman & Kjerfve, 2008).

3.4.3. Size, age, and maturation structure of mutton snapper

The biological variables of mutton snapper evaluated in this study from reproductive individuals harvested at Gladden Spit during one annual fishing season (March-June 2011) are in agreement with the characteristics reported for the species across its geographic range. As a gonochoristic species, adults have no significant variation in size between sexes and populations have F:M ratios close to unity (Erhardt and Meinel, 1977; Claro, 1981; Burton, 2002; Claro and Lindeman, 2004). Typical of Lutjanids, the Brody growth coefficient estimated for mutton snapper from this study was relatively low ($K=0.13*year^{-1}$) and concordant with the $K<1.5*year^{-1}$ expected for the species (Mason and Manooch, 1985; Burton, 2002; Claro and Lindeman, 2004; SEDAR, 2008). Although length and age at maturity were not estimated using population models, it was determined that >50% of the individuals landed at Buttonwood Caye were mature at 490 mm TL for males and at 520 mm TL for females, values that correspond with age 4 for both sexes. This finding is consistent with that of Claro (1981) who noted that for mutton snapper in Cuba, males mature earlier than females. While the ranges of length and age at maturity for the species vary with geographic location and season and have been projected to 400-500 mm TL and 4-6 years (Allen, 1985; Claro and Lindeman, 2004; SEDAR, 2008), mutton snapper can reach sexual maturity as soon as 2-3 years, with sizes of 320 mm TL for males (Erhardt and Meinel, 1977) and 353 mm TL for females (SEDAR, 2008). Data from this study confirms this for the species and illustrates it for Belize, as the smallest mature individuals landed were a male of 330 mm TL and a female of 380 mm TL (age 2 for both).

The age of mutton snapper determined by otolith microstructure techniques in this study ranged between 2 and 16 years and is concordant with previous studies (e.g., Mason and Manooch, 1985; Burton, 2002; Claro and Lindeman, 2004). Despite recent studies raised the maximum age for mutton snapper to 40 years (SEDAR, 2008), the maximum age (50 years) projected by the VBGE model in this study needs to be interpreted with caution and validated by further studies. The parameters of the VBGE model in this study were estimated without including sizes and ages from juvenile and sub-adult individuals. Therefore, the VBGE model in this study will tend to underestimate age when TL approaches 0 mm and to overestimate age when TL approaches mean asymptotic length (L_∞).

Across the species range, the peak of the reproductive season of mutton snapper varies with geographic location. Mutton snapper spawning aggregations peak in May-June at Riley's Hump in the Dry Tortugas, Florida (Domeier and Colin, 1997; Lindeman et al., 2000; Burton et al., 2005), April-May in West Caicos, Turks and Caicos Islands (Domeier et al., 1996), either May or June in Cuba (Claro, 1981; García-Cagide et al., 2001; Claro and Lindeman, 2003, 2004), and April-June in Puerto Rico (Matos-Caraballo et al., 2006a). Mutton snapper are reproductively active all year in Northeastern Brazil (Teixeira et al., 2010). Though spawning aggregations of mutton snapper are known to occur between February and September at Gladden Spit (Heyman and Kjerfve, 2008), it has traditionally been known to peak in March-June. Though mutton snapper landings at Buttonwood Caye were minimal in March 2011 compared to yellowtail snapper (10 mutton vs. 15,752 yellowtail snapper landed that month), SEA divers recorded a maximum number of 3,500 mutton snapper and 2,000 yellowtail snapper during SCUBA underwater visual censuses (UVC) at Gladden Spit (Granados-Dieseldorff, 2012). Other than verifying that mutton snapper did aggregate at Gladden Spit in March 2011, this information should be interpreted with caution as several sampling, methodological, and data limitations precluded the use of UVC data in combination with landings data in 2011 (Granados-Dieseldorff, 2012).

During the protracted reproductive period of snappers, the size and age structure of reproductive individuals, as well as their degree of maturation, vary with geographic location and throughout the reproductive period (Grimes, 1987; García-Cagide et al., 2001; Claro and Lindeman, 2004; Jackson et al., 2007). Despite the limited duration of this study, the minimal catches of mutton snapper in March, and the lack of annual replications, data showed a distinctive size structure of catches between April and June, with individuals significantly smaller and younger in June. Studies on mutton snapper spawning aggregation fisheries in Florida and Cuba corroborate this finding (Claro, 1981; Lindeman et al., 2000; García-Cagide et al., 2001; Claro and Lindeman, 2004). Sizes of mutton snapper aggregating to spawn closer to the Florida Keys are smaller than those aggregating in deeper waters and in later months of the spawning season (Lindeman et al., 2000). Along the insular shelf of southern Cuba, where mutton snapper spawning aggregations also peak in May as in Florida and this study, sizes of individuals were significantly smaller at the same aggregations sites in June (Claro, 1981; García-Cagide et al., 2001). The same decreasing trend in mutton snapper sizes along the spawning season also happens in the northern insular shelf of Cuba, yet the peak of the mutton snapper spawning aggregations happens one month later (June) in that region (García-Cagide et al., 2001; Claro and Lindeman, 2004).

Given that fecundity of female mutton snapper is age structured and that their fertility varies among size classes (Clarke et al., 1997; Watanabe, 2001; Claro and Lindeman, 2004; SEDAR, 2008), it is difficult to estimate with the data from this study the potential loss of offspring from harvested individuals to fishing. Nevertheless, based on the reproductive biology of mutton snapper and the CPUE, female GSI and corresponding degree of maturation (gonad state, Type I-IV) determined in this study, it is very likely that most of the females that were landed in June 2011 did not have the chance to spawn. Though mutton snapper females can reach sexual maturity at (2-3 years), 380 mm TL (age 2) in this study, the length at maturity of females set for sustainable harvest by stock assessments continues to range between 400 and 500 mm TL (4-6 years) (Claro and Lindeman, 2004; SEDAR, 2008). In this study, most females were mature at 520 mm TL (4 years). However, in June alone, 66.4% of females were in Type I gonad state (480 mm TL; 4 years). Considering that mutton snapper females spawn periodically and frequently during their protracted reproductive period (García-Cagide, 2001; Claro and Lindeman, 2004), a precautionary approach that limits fishing in June at Gladden Spit is warranted, so females that aggregate in June and subsequent months increase their chances of reproduction.

3.4.4. Considerations for management

For over 60 years, artisanal fishers from Belize have targeted the mutton snapper spawning aggregations and the associated reef fish assemblage at Gladden Spit (Chapter II). Through the declaration of the GSSCMR in 2000 (Government of Belize, 2000) and the creation and gradual implementation of fishing regulations since 2003 (Government of Belize, 2003a, b), co-management has sought to protect Gladden Spit's multi-species spawning aggregations, while also allowing the historical mutton snapper fishery to maintain its traditional operation. Although the mutton snapper fishery at Gladden Spit has historically been multi-species, its management continues to be single-species oriented and attention has been diverted from other target and nontarget species, such as yellowtail snapper that numerically outweighed in landings in 2011 and the other 48 reef fish species that were incidentally caught with hand lines throughout the fishing season (March-June). Given the interactions between seasonal assemblages of co-occurring reef fishes with the local dynamics of artisanal multi-species fisheries, such as it was the case for the mutton snapper fishery in this study, it is imperative to understand fishing operations and to identify the potential impacts on both the target and nontarget species for their effective management (Medley et al., 1996; Salas et al., 2004; Monroy et al., 2010).

Fishery regulations established with the declaration of GSSCMR closed the multi-species spawning aggregation to fishing except for allowing licensed traditional fishers to harvest the mutton snapper spawning aggregations in March-June every year and only during daylight hours (Government of Belize, 2003a, b). With effective enactment and enforcement, these regulations should grant protection to mutton snapper spawning aggregations outside the fishing season (i.e., July-September) and to other species that aggregate to spawn at other times of the day and year as discussed previously in this chapter and elsewhere (Chapter II). However, this study suggests that in addition to impacting numerous reef fish species and a considerable period of the yellowtail snapper spawning aggregations at Gladden Spit, the fishing activity in June is affecting an important stage in the reproductive period of mutton snapper.

Because of the high fish diversity in coral reef ecosystems, management of bycatch is inherently complex, even for handline fisheries (Medley et al., 1993; Serafy et al., 2012; Johnson et al., 2013). This is especially true for dense congregations of fishes at Gladden Spit and other sites of the tropical Western Atlantic where hooks from hand lines lose both species and size selectivity (Claro and Lindeman, 2003; Matos-Caraballo et al., 2006b; Patterson et al., 2012) . Moreover, the losses to barotrauma of bycatch species in deep water fisheries preclude the implementation of strategies such as bycatch return to the ocean and size limits for protecting immature stages. However, it is evident that much of the fishing impact on mutton snapper and bycatch species occurs early and late in the fishing season (i.e., March and June). During their frequent community consultations (see Chapter II), co-managers, fishers, and other stakeholders could consider shortening the duration of the fishing season in order to reduce fishing pressure at Gladden Spit in March and June, and with that, alleviate the impact on yellowtail snapper spawning aggregations, juvenile bycatch species, and immature mutton snapper.

As argued in Chapter II, the current co-management structure adopted for the conservation of GSSCMR could offer a platform for cooperation among co-managers, fishers, and rest of stakeholders in resource and market management, monitoring, evaluation, and decision making. Although the assessment of this co-management structure and its influence on the mutton snapper fishery was not among the objectives of this chapter, stakeholder-centered constituencies for managing marine resources in the tropics, rather than top-down mandated strategies, are considered key for the sustainability of small-scale fisheries (Defeo and Castilla, 2005; Berkes, 2012; Cinner et al., 2012). Stakeholder-centered approaches to small-scale fisheries can also be important when the socio-environmental sustainability of fisher-fish systems, as defined in Chapter II, is dependent upon the articulation of the assemblage of target and nontarget fish species, the local livelihoods of fishes, and the market system that governs demand and hence influences extraction.

3.5. Summary

Since the 1950s, artisanal fishers have harvested mutton snapper (*Lutjanus analis*) at Gladden Spit, southern Belize Barrier Reef. The fishery targets the peak of the species spawning aggregations, which recurs annually in March-June, 10-12 days around the full moon days. In order to describe the within-season dynamics of the mutton snapper fishery and its associated bycatch and characterize for the first time the size, age, and maturation structures of reproductive mutton snapper at Gladden Spit, I sampled the landings of the fishery between -2 and 7 days relative to full moon (drfm) in March-June

2011. I identified 18,709 bycatch fish from 49 different species and measured, weighted, and macroscopically examined the gonad state of 5,047 mutton snapper from which sagittal otoliths were randomly collected (n=115). The monthly fishing dynamics were influenced by the reproductive behavior of mutton snapper, interaction with other co-occurring fisheries, and by the fishers' traditions. Mutton snapper constituted only 21.2% of the fishery landings in numerical abundance. Relative abundances of the species varied significantly in relation to drfm and among months. Significant monthly variations in the size, age, and maturation structures of aggregating individuals were detected, with older individuals dominating in March-May, while younger individuals in June. Most males were mature throughout the season, while most females were predominantly immature in June. Results suggest that the reproductive output from mutton snapper that aggregate to spawn at Gladden Spit is seasonally structured and that most females harvested in June 2011 missed their chance to spawn.

CHAPTER IV

A GIS-BASED MODELING APPROACH TO LOCATE SUITABLE JUVENILE HABITAT FOR MUTTON SNAPPER (*Lutjanus analis*) ACROSS THE BELIZE SHELF

4.1. Introduction

The early life-history stages of tropical coral-reef fishes play an important role in the dynamics that regulate and maintain their population abundance (Ehrlich, 1975; Sale, 1998). These stages are generally classified into two distinct phases: a pelagic phase phase that includes eggs and larvae, followed by a demersal phase that includes juveniles and sub-adults. The two phases are coupled when demersal adults spawn pelagic eggs and when larval survivors or pelagic juveniles settle into nursery environments (Doherty et al., 1985; Leis, 1991; Sale, 1998). Settlement generally occurs parallel to physical metamorphosis across different habitats.

Fundamental to conservation and management of Caribbean reef finfish fisheries is understanding relationships between population regulation and habitat use throughout the ontogenetic development of fishes (Medley et al., 1993; Lindeman et al., 2000; Rubec et al., 2001). In addition to biological and oceanographic factors, coastal development and fishing pressure can affect multiple life-history stages of Caribbean reef fishes and therefore impact population size (Bohnsack and Ault, 1996; Lindeman et al., 2000; Ault et al., 2005). Holistic approaches that integrate biological, oceanographic, habitat, and anthropogenic factors have been proposed for effectively managing Caribbean reef fisheries (Lindeman et al., 2000; Lorenzen et al., 2010; Fanning et al., 2011). Yet, most management and regulatory approaches continue to focus on single environmental (e.g., habitat type), biological (e.g., a species or life-history stage), or operational (e.g., fishing gear type or season) factors and frequently miss critical components that are also important to sustained exploitation in multi-species fisheries.

In Belize and rest of the Caribbean, mutton snapper (*Lutjanus analis* Cuvier 1828, family Lutjanidae) is an ecologically important and highly valuable reef fishery species (Allen, 1985; Claro and Lindeman, 2004; Chapter III). Typical of reef fishes, mutton snapper use various habitats during their life cycle. Because of the high demand for its meat, the threat from the unregulated harvest of their spawning aggregations, and the weak management of their commercial and recreational fisheries at several locales of the Caribbean, mutton snapper are considered to be vulnerable to extinction by the List of Threatened Species of the International Union for Conservation of Nature and Natural Resources (Huntsman, 1996). In order to protect the marine habitats and the spawning aggregations of mutton snapper and other ecologically and economically important reef fishes, the Government of Belize, with support from several community-based nongovernment organizations, created a network of marine protected areas along the Belize Barrier Reef (Government of Belize, 2003a,b; Gibson et al., 2004; Walker and Walker, 2011). Spawning aggregation sites are co-managed as non-extractive zones where fishing is banned during the entire, with a few exceptions (Government of Belize, 2003 a,b; Heyman, 2011; Chapter II).

Studies of mutton snapper in Belize are concentrated on the Gladden Spit spawning aggregation site. Fishery-dependent data of adults harvested from Gladden Spit have been evaluated (Graham et al., 2008; Chapters II and III) and the courtship and spawning of reproductive individuals have been described (Heyman and Kjerfve, 2008). No information exists on other life history stages of mutton snapper across the Belize shelf. To begin to fill this critical gap in the literature on this species, I developed and evaluated in the field (*sensu* Grant and Swannack, 2008) a GIS-based habitat suitability model for juvenile mutton snapper in Belize and assessed the degree of protection afforded to suitable habitats. The model was conceptualized and parameterized based on the general ecology of mutton snapper and on the availability of open-access GIS data for the area. I assumed that the main factors determining habitat suitability of the species across the Belize shelf included: 1) distance to spawning aggregation sites, 2) habitat type, 3) level of riverine pollution, and 4) and stress from fishing activities to benthic habitats. The model's projections were evaluated against mutton snapper presence-absence data collected using underwater visual census in 2009.

4.2. Material and methods

4.2.1. Study area

The Mesoamerican Barrier Reef stretches 1,000 km along the Caribbean coasts of Mexico, Belize, Guatemala, and Honduras (Fig. A.1.19) and is a highly biodiverse marine ecoregion of global conservation importance (Roberts et al., 2002; Spalding et al., 2007). The Belize shelf hosts most of the Mesoamerican Barrier Reef and also constitutes the western boundary of the tri-national Gulf of Honduras (Heyman and Granados-Dieseldorff, 2012). The network of marine protected areas in Belize continues to be exemplary across the Caribbean for its coverage of spawning areas and extent of co-management (Gibson et al., 2004; Pomeroy et al., 2004; Walker and Walker, 2011).

Coastal Belize encompasses a network of estuarine and marine habitats that several reef species use during their ontogenic development (Gibson et al., 1998; Heyman and Kjerfve, 1999). West of the barrier reef, between the shoreline and the back reef areas, a coastal lagoon harbors mangroves, seagrass beds, sand cayes, and patch reefs. East of the barrier reef, the deeper shelf encompasses the pelagic and abyssal zones of the Gulf of Honduras, western Caribbean (Fig. A.1.19).

The climate and hydrometeorology of the region are controlled by the easterly trade winds and their interactions with the annual variability of the intertropical convergence zone (Heyman and Kjerfve, 1999; Thattai et al., 2003). Local weather is also controlled by the orographic effects from the central mountain ridge of Central America. Air and surface water temperatures vary with season, with values fluctuating between 27 and 31^{o} C throughout the year. A pronounced dry and wet seasons are characteristic of the region, with precipitation maxima in June-October and minima in February-April. Total mean annual precipitation is generally high, ranging from 1,500 mm in northern Belize to 5,000 mm in the south (Heyman and Kjerfve, 1999; Thattai et al., 2003).

The coastal lagoon (Fig. A.1.19) receives riverine outflow and coastal runoff from the continental watersheds of Honduras, Guatemala, Belize, and Mexico (Heyman and

Kjerfve, 1999; Thattai et al., 2003; Burke and Sugg, 2006). Freshwater input creates marked onshore to offshore gradients in salinity, dissolved oxygen, and suspended sediments. Freshwater and sediment inputs to the lagoon are directly related to the volume of run-off and sediment load carried by coastal rivers, which in turn are related to the levels of precipitation in the adjacent continental watersheds (Thattai et. al., 2003; Burke and Sugg, 2006). In the southern region of the coastal lagoon, freshwater and sediment input are increased by the presence of several major tributary watersheds that are hydrologically separated from the northern lagoon around the Placencia Peninsula (Heyman & Kjerfve, 1999; Thattai et. al., 2003).

4.2.2. Study species

Mutton snapper (*Lutjanus analis* Cuvier 1828, Lutjanidae) is a long-lived, reef-associated, and highly valuable fishery species that is distributed across the subtropical and tropical waters of the western Atlantic Basin, from Massachusetts, USA, to Sao Paulo, Brazil, including the Caribbean (Allen, 1985; Mason and Manooch, 1985; Claro and Lindeman, 2004). As a euryhaline and eurythermal fish, mutton snapper undergo seasonal and ontogenic habitat shifts throughout their development and growth, during which they encounter different environmental conditions, prey, and predators. During their settlement and juvenile stages, mutton snapper inhabit mangrove estuaries and sandy bottoms covered with sea grass. As adults, they migrate offshore to coral reefs and other complex benthic hard habitats for reproduction (Allen, 1985; Claro and Lindeman, 2004). Their pelagic phase starts when eggs are fertilized in the water column, usually at site-specific spawning aggregations (Fig. A.1.20). Egg fertilization and metamorphosis occurs 24-48 h after hatching and the larval stage lasts another 11-12 d (Clarke et al., 1997; Watanabe, 2001; Lindeman et al., 2006). Settlement and metamorphosis to the juvenile stage in demersal nursery habitats begins 13-19 d after hatching (Fig. A.1.20), at 110-160 mm total length (TL) (Lindeman et al., 2006). As gonochoristic fish, they reach sexual maturity as males and females as soon as 2 years in Belize (Chapter III), but typically at 4-6 years throughout the species geographic range (Claro and Lindeman, 2004).

Mutton snapper are rarely found in groups, except during spawning migration events (Allen, 1985; Claro and Lindeman, 2004) and are thus classified as a species that spawns in transient fish spawning aggregations (Domeier and Colin, 1997). Mutton snapper aggregate to spawn in at least five sites along the Belize Barrier Reef (Heyman and Kjerfve, 2008; Kobara and Heyman, 2010; Chapter II) including: Caye Bokel, Glover's Long Caye, Gladden Spit, Seal Caye, and the Rise and Fall Bank (Fig. A.1.19).

4.2.3. GIS-based model

4.2.3.1. GIS data collection

GIS themes from the Mesoamerican Barrier Reef were selected from an extensive data search across several public oceanographic, climatic, and environmental metadata sites for GIS-processed features and rasters (Table A.2.7). Searched sites included the National Oceanographic Data Center (NODC, 2008), the National Climatic Data Center (NCDC, 2008), the SeaWiFS Data Analysis System (SeaDAS, 2008), the Land Processes

Distributed Active Archive Center (LPDAAC, 2008), the National Geophysical Data Center (NGDC, 2008), the MesoStor Database of the *Sistema Regional de Visualización y Monitoreo de Mesoamérica* (SERVIR, 2008), the Biodiversity and Environmental Resource Data System of Belize (BERDS, 2008), and the Watershed Analysis for the Mesoamerican Reef Database (Burke and Sugg, 2006).

Most of the selected input data were obtained from BERDS (2008) and Burke and Sugg (2006) and had a spatial reference set to the NAD 1927 UTM projection (UTM, Zone 16 North, NAD 27 Central) and other data were re-projected to be consistent. The spatial extent of the analyses was set to the derived shapefile of the marine habitats of Belize (BERDS, 2008) and the cell size set to 100 m (Fig. A.1.21).

4.2.3.2. Model assumptions

Several snapper species aggregate to spawn in sites that are close to reef patches and barrier reefs with a suite of oceanographic attributes that have presumably favored this reproductive behavior during their evolutionary history (Grimes, 1987; Martínez-Andrade, 2003; Claro and Lindeman, 2004). After spawning in aggregations, mutton snapper eggs and larvae are then believed to drift away from the spawning sites with oceanic currents, ultimately to settle as juveniles in nursery habitats, mainly mangroves and seagrass beds, approximately three weeks after spawning (Fig. A.1.20). Considering these general characteristics of the life cycle of mutton snapper and the availability of GIS data for parameterizing the habitat suitability model in this study (Table A.2.7), the model assumptions were: 1) mutton snapper aggregate to spawn mainly at Caye Bokel, Glover's Long Caye, Gladden Spit, Seal Caye, and the Rise and Fall Bank; 2) surviving larvae will recruit and settle into mangrove and seagrass habitats in the coastal lagoon, and 3) anthropogenic stresses over marine ecosystems, such as continental pollution and pressure over benthic habitats from fishing activities (fishing pressure, hereafter), detrimentally affect settlement of juvenile mutton snapper.

4.2.3.3. Model parameterization

Following Eastman et al. (1995) and Aly et al. (2005), a GIS-based weighted multi-criteria evaluation function was used to geostatistically quantify and spatially project habitat suitability. The most relevant procedure for multi-criteria evaluation is the weighted linear combination (Voogd, 1983). In a weighted linear combination, factors are combined by applying a weight to each, followed by a summation of the results that yields to a map of suitability (Eastman et al., 1995). The weighted linear combination used to parameterize the model in this study was:

$$S= \Sigma (w_i*x_i),$$

where (S) is suitability of sites expressed as the sum of multiple parameters (criteria) in consideration, (i) a parameter considered in the spatial model, (w) a weight assigned to parameter (i) based on the model assumptions, and (x) a geostatistically-corrected correlation weight for parameter (i), expressed as an eigenvalue.

Based on the model assumptions (see 4.2.3.2), four different parameters (i) were selected for predicting habitat suitability across the Belize shelf (Fig. A.1.21): marine habitat type (MHT), distance from spawning aggregations sites (DSA), fishing pressure gradient (FPG), and continental pollution gradient (CPG). I used the ModelBuilder application in ArcGIS 9.2 (ESRI, 2007) and Spatial Analyst (ESRI, 2001) to geoprocess input data into quantifiable raster parameters (Table A.2.7; Fig. A.1.21). Weight of raster parameters (w) were assigned from 1 (unsuitable) to 4 (highly suitable).

For CPG, buffer analyses at 10-, 20-, 30-, and 40 km distance intervals were performed from the mouths of rivers with high sediment discharges, simulating dispersal of sediments and pollutants with increasing distance from river mouths (Thattai et. al., 2003; Burke and Sugg, 2006). Areas distant from river mouths received the highest suitability scores (4). A similar procedure was used to quantify DSA, with areas closest to the five mutton snapper spawning aggregation sites receiving highest scores. The parameterization of MHT was based on the life cycle of mutton snapper (Fig. A.1.20) and followed this classification: pelagic (open-ocean) habitats were assumed as suitable only for eggs, larvae, and adults and hence received the lowest score (1); seagrass and mangrove habitats were assumed as highly suitable for juveniles (score=4), followed by littoral forests (3), and benthic algae beds (2). Finally, FPG was parameterized based on the geographic classification of commercial finfish fisheries yields by the Belize Fisheries Department. The Belize Fisheries Department classifies fishing grounds as a function of catch yields, expressed as catch per unit effort (CPUE). It was assumed in this model that stress over natural marine habitats and fish densities increased with greater CPUE, with weights fluctuating between 1 (greatest CPUE values) and 4 (lowest CPUE values).

The WEIGHT decision support module in IDRISI-Andes (Eastman, 2006) was used to solve the multi-criteria weighted linear combination. WEIGHT utilizes an analytical hierarchy process to compute a best-fit set of weights through a pairwise comparison of factors in a multi-criteria evaluation. In this procedure, continuous criteria (i.e, factors) are standardized to a common numeric range, and then combined by means of a weighted average (Eastman, 2006). The output is a continuous mapping of suitability that may then be masked by one or more Boolean constraints (i.e., suitability scores, 1-4) to accommodate qualitative criteria, and finally yield to a final decision (i.e., unsuitability or suitability).

Before mapping habitat suitability, a pairwise comparison matrix was built through subjective assignments of relative weights in order to assess the degree of consistency with which the weights were assigned. Saaty (1977) introduced a procedure by which an index of consistency, known as a Consistency Ratio (CR), can be produced. This CR indicates the probability that the matrix judgments were randomly generated, whereby a CR ≤ 0.10 is considered a reasonable level of consistency. Raster Calculator in Spatial Analyst (ESRI, 2001) was then used to incorporate the weights from the weighted-linear combination into a raster calculation that would derive a new raster file from the WEIGHT output. The final raster was reclassified and geoprocessed to select only for locations with the highest suitability indices and produce a map of the distribution of suitable habitat for juvenile mutton snapper across the Belize shelf.

4.2.4. Model evaluation

The model's projections of juvenile mutton snapper habitat suitability were evaluated in the field (*sensu* Grant and Swannack, 2008) in 2009. Underwater visual censuses (UVCs) were conducted along 2x30 m belt transects along seagrass-mangrove ecotones across the southern Belize shelf. Considering that freshwater and sediment input into the Belize lagoon increases southward and that the Placencia-Gladden Spit transect is the geographical boundary between regions of low and high precipitation (see 4.2.1.), sampling was segregated into 1) the South region, east of Punta Gorda and 2) the North region, east of Placencia (Fig. A.1.19).

Following a nested sampling design (Underwood, 1997), two eight-day collection trips in the peaks of the dry (April) and rainy (July) seasons were conducted, with the intention of sampling the peak settlement season of mutton snapper in the area. In each sampling region, UVC data were collected at three strata across the lagoon: inner lagoon (close to the shoreline), mid lagoon, and outer lagoon (close to the back reef). Each of the six strata had three replicate stations, for a total of 18 stations that were sampled twice (April and July) across the southern Belize shelf. At every sampling station, three belt transect replicates were conducted along mangrove props and three other replicates along seagrass beds located 15 m offshore and parallel to the shoreline (n=648 belt transects). Since mutton snapper recruit into nursery habitats at 110-150 mm TL (see 4.2.2.), only individuals < 100 mm TL were recorded. Since mutton snapper typically occur in these habitats in association with other snapper species (Claro, 1981; Claro and Lindeman, 2004), all snapper species in juvenile stage (i.e., TL<100 mm) were also recorded.

4.3. Results

The model indicated that marine habitat type (MHT), distance from spawning aggregation sites (DSA), fishing pressure gradient (FPG), and continental pollution gradient (CPG) individually affect the distribution of suitable habitat across the Belize shelf (CR=0.07; Fig. A.1.22). The WEIGHT analysis resolved four inter-correlated parameters (Table A.2.8) that explained the weighted linear combinations as follows:

$$S = 0.56*(MHT) + 0.27*(DSA) + 0.10*(CPG) + 0.07*(FPG).$$

Based on the parameterization of the model, 56% of the suitable habitat for mutton snapper projected across the Belize shelf was explained by MHT, 27% by DSA, 10% by CPG, and 7% by FPG. The model projected suitable habitat in areas with sea grasses, around coral reefs, or a combination of both (Fig. A.1.23). The total area of the projected suitable habitat was 2,408.7 km^2 and only 209.4 km^2 of this area (8.69%) was located inside marine protected areas (Figs. A.1.23 and A.1.24).

Of the 18 sampling stations surveyed during the field evaluation (March and July 2009), seven were inside projected suitable habitat and 11 outside (Fig. A.1.24). Four of the stations where mutton snapper were recorded were located in areas of projected suitable habitat. A total of 1,007 juvenile snappers (TL<100 mm) from eight species were identified along 648 underwater belt transects (Table A.2.9). Along with mutton snapper, dog snapper (*Lutjanus apodus*), yellowtail snapper (*Ocyurus chrysurus*), and cubera snapper (*Lutjanus cyanopterus*) spawn in multi-species spawning aggregation sites along the Belize Barrier Reef (Heyman et al., 2005; Heyman and Kjerfve, 2008; Kobara and Heyman, 2010).

4.4. Discussion

Using a common spatial framework, this study illustrated how data on life history, habitat type and distribution, and anthropogenic stressors can be evaluated and used to synthesize conservation and management guidance for mutton snapper in Belize. Specifically, habitat type and distance from spawning aggregation sites controlled together 83% of the spatial variability of suitable habitat for mutton snapper in Belize. The modeling approach in this study also provided a platform for rapidly evaluating the degree of protection granted to essential juvenile habitats of mutton snapper and other snapper species and can also serve as a tool for decision making in the placement of marine protected areas (MPAs) and the spatial management of habitats across the Belize shelf.

The ecology of mutton snapper, as it is for most coral reef fishes, is conspicuously complex and multi-scalar. Scales are set by the life history of the species and by the spatial structure of the seascape in which they live (Sale, 1998). The scale of egg and larval dispersal is one of the greatest and most crucial unknowns impacting efforts to design effective MPA networks (Bohnsack, 1998; Sale et al., 2005, Steneck et al., 2009). For example, the time between spawning and complete settlement of most Caribbean snappers usually does not exceed 3-4 months, whereas their juvenile and adult stages commonly span 4-40 years (Claro et al., 2001; Claro and Lindeman, 2003, 2004). Fine-scale information on the demersal life stages and their distribution across the shelf is limited for almost all species throughout the Western Caribbean. Though the projected distribution of suitable juvenile habitat of mutton snapper across the Belize shelf in this study is hypothetical, the model situated settlement areas inside the coastal lagoon and atoll lagoons along the Barrier Reef. Only 8.69% of this hypothetical area was inside of MPAs. On the contrary, all of the 11 currently active multi-species spawning aggregations along the Belize Barrier Reef are protected (Government of Belize, 2003 a,b). This contention in the current spatial arrangement of MPAs is important to consider because, as protected spawning aggregation sites can serve as concentrated sources of eggs and larvae, unprotected settlement areas and degradation of nursery habitats can detrimentally affect the abundance of future spawners. Considering the complex, multi-scalar nature of reef fish species that aggregate to spawn, the spatially discrete habitat projection of this study model can be used to pinpoint focal areas that deserve special consideration for habitat and fisheries management.

The heuristic and qualitative nature of this model, however, presented several limitations and precluded formal sensitivity and statistical analyses for testing its validity. Other oceanographic variables (e.g., bathymetry, currents flows and directions, high-resolution sea surface temperatures, salinity, location of gyres) and hydrological data (e.g., sediment discharges of the watersheds from the other countries sharing the Mesoamerican Barrier Reef) could improve the prediction power of a reformulated version. The degree of use of nursery habitats needs also to be investigated and, if expressed in standardized indices (e.g., recruitment indices), they could be important inputs for the model. Finally, demographic and population factors (e.g., density dependence, predation, competition) that can affect the densities of larvae and settlers of mutton snapper in Belize were not considered since information on the biology of the species is sparse and differs with location throughout the species range (Claro and Lindeman, 2004; Chapter III).

Mutton, dog, yellowtail, and cubera snapper share several multi-species spawning aggregation sites along the Belize Barrier Reef (Kobara and Heyman, 2010) and during the warmer months of the year (Heyman and Kjerfve, 2008; Chapter II). The species share similar life history strategies (Allen, 1985; Martínez-Andrade, 2003; Claro and Lindeman, 2004). Hypothetically, at a broad scale of observation, their larvae should have similar chances of recruiting into same settlement areas across the Belize shelf. Interestingly in this study, species densities and distributions of these taxa across the southern Belize Shelf were uneven. More importantly, mutton snapper counts in UVCs were low. Future field sampling for determining juvenile snapper abundances should 1) encompass other areas along the coastal lagoon and across the shelf of Belize, 2) survey other times of the year, and 3) employ alternate collection methods for efficiently estimating abundance. Juvenile mutton snapper recruit mainly to shallow estuarine bays with seagrass bottoms in the Cuban shelf (Claro, 1981). Furthermore, as recruits tend to be segregated and hidden among sea grasses, they are difficult to detect by UVC (Claro and Lindeman, 2004). Surveys of abundance using passive collection methods might be more efficient in vegetated sandy benthic habitats. More importantly, abundance of mutton snapper recruits in Cuba commonly peak in August-October (Claro, 1981; Claro and Lindeman, 2004) and if this is the pattern in Belize, this would explain the low counts of mutton snapper in UVCs.

The GIS-based model in this study should be considered as an adaptive tool (*sensu* Walters, 1986) that facilitates decision making in complex situations in marine spatial and fisheries management. By using popular GIS platforms (e.g., ArcGIS and IDRISI-Andes), the conceptual model is versatile, replicable, and manageable. This model can also be re-evaluated, re-parameterized, and re-run as more data become available. Among its applications, the modeling approach in this study can also be used to evaluate the degree of habitat connectivity when designing MPA networks, not only across the Belize shelf, but also in other regions of the Caribbean with similar geomorphological and habitat attributes. Developing a relatively free spatial GIS-based modeling tool and making it accessible to the public through BERDS or other databases, could considerably contribute to the conservation and management of mutton snapper and other important reef fisheries in the area.

4.5. Summary

Because of their complex life history ecology, management of reef fisheries is challenging. Locating suitable marine and coastal habitats for fishes in the Caribbean involves complex judgments that are important for the design of effective networks of marine reserves. In order to evaluate the hypothetical distribution and spatial management of suitable habitat for juvenile mutton snapper (*Lutjanus analis*) across the Belize shelf, I developed a GIS-based habitat suitability model. The analysis used raster data within a weighted multi-criteria model using ArcGIS 9.2 and IDRISI Andes. Free-access GIS themes with associated metadata from Belize were collected online. Data

were then organized and geoprocessed into the model's raster inputs. Evaluated ecosystem parameters (i.e., raster inputs) included marine habitat type, distance from spawning aggregation sites, fishing pressure gradient, and continental pollution gradient. Potential juvenile habitat encompassed 2,408.7 km^2, but only 8.69% of this area was located inside marine reserves. Using a common spatial framework, this model illustrated how data on life history, habitat type and distribution, and anthropogenic stressors can be synthesized to guide conservation efforts for Lutjanids in Belize. The spatially discrete model also provided a platform for marine spatial planning and management of the Belize shelf, evaluating the degree of protection granted to essential juvenile habitats for mutton snapper, and pinpointing focal areas that deserve special consideration or protection.

CHAPTER V

SUMMARY AND CONCLUSIONS

The three overall goals of this dissertation were to 1) present a retrospective analysis of the history of the mutton snapper (*Lutjanus analis*) fishery at Gladden Spit in its environmental and socioeconomic context, 2) describe the within-season dynamics of the fishery in 2011, and 3) evaluate the potential distribution of suitable habitat for juvenile mutton snapper across the Belize shelf. As an in-depth case study, this dissertation explored a suite of methods that can be followed to analyze inter-annual and within-season dynamics of data-poor, small-scale fisheries that target spawning aggregations of Lutjanids and to evaluate the geographical arrangement of their early-life history habitats, critical for maintaining their populations. The results can be used to assess, redefine, or strengthen established conservation and management strategies for aggregating fisheries of Lutjanids in Belize and complement the information on the biology of mutton snapper and the ecology of their fisheries in the western Atlantic.

Chapter II portrayed the socio-environmental history of the artisanal mutton snapper fishery at Gladden Spit. The fishery commenced as a subsistence fishery in the early 1950s but became more commercially oriented in the 1970s when ice became available in the region and facilitated better preservation of catches. Mutton snapper landings surged in the early 1980s with the introduction of motorized Mexican-style skiffs to Belize that allowed more efficient catches and reduced transportation time to the mainland. Both catch and fishing effort declined sharply in the late 1980s, in parallel to a rapid growth in the tourism industry and a shift in the livelihoods of many fishers. Annual catch per unit effort (CPUE), individual sizes, and sex ratios were relatively stable between 1999 and 2011, indicating persistence of the fishery during this recent period. Similar to other persistent Caribbean mutton snapper fisheries, the biology and life-history strategies of the species, the oceanographic conditions at Gladden Spit, and the proximity of other protected spawning sites and nursery areas may confer the fishery special resilience to present levels of exploitation, distinct and in contrast to other aggregating fisheries.

Chapter III depicted the within-season fishery dynamics for 2011. Since fishers have traditionally targeted these mutton snapper spawning aggregations during the peak of their reproduction period (i.e., March-June), it was possible to use their landings to assess the size, age, and maturation structures of reproductive individuals aggregating at Gladden Spit. To the best of my knowledge, this has been done only for two aggregating mutton snapper fisheries in the Cuban continental shelf. Therefore, this chapter fills an important gap of crucial information in the biology of mutton snapper that needs to be considered in the species fisheries management across the western Atlantic. Analyses from 5,047 mutton snapper individuals showed how fishing effort, catches, CPUE, as well as fish size, age, and degree of maturation fluctuated around the days of full moon and significantly differed among months. Sizes of mutton snapper harvested at Gladden Spit in 2011 ranged between 315-905 mm TL, weights 0.5-11.8 kg, otolith-based ages 2-16 years, and projected ages, by a von-Bertalanffy-growth-model equation, 2 to >30 years. Also, distinctive size and age structures were evident. Size and age classes progressively decreased with the ongoing fishing season. Both male and female mutton snapper were significantly smaller and younger in June than in April or May. It is very likely that most of the females that were caught in June (2011) missed their chance to spawn.

Chapter III also reported a list of 49 bycatch species, 14 of which are known to aggregate to spawn at Gladden Spit. Particularly interesting was the significant harvest of yellowtail snapper (*Ocyurus chrysurus*), another species that forms transient spawning aggregations but that has escaped consideration from conservation agencies. Between March and June 2011, mutton snapper constituted only 21.2% of the fishery landings in numerical abundance, 42.6% in biomass, and 60.6% in total profits; whereas yellowtail snapper represented 67.4% in abundance, 44.3% in biomass, and 35.9% in total profits. Since yellowtail snapper likely aggregated also to spawn at Gladden Spit, this represents a rapidly increasing fishery of another, yet unmanaged, aggregating fishery at the site. Overall, Chapter III illustrated how monthly fishing dynamics were influenced by the reproductive behavior of mutton snapper and by the fishers' traditions. The fishery fleet composition varied significantly among months in response to fishers' alternate occupations, compliance with fisheries laws, and harvest of other commercially important species, such as yellowtail snapper in March and the highly lucrative lobster (*Panulirus argus*) fishery in June. Chapter III also revealed a shift from a traditional market and purchase power locally controlled by fishers, to a recent Caribbean trade of artisanal fisheries managed by major international corporations and that demanded mutton snapper, yellowtail snapper, and most of the other 48 bycatch fish species.

After focusing on the adult stages of mutton snapper in chapters II and III, the GIS-based multi-criteria modeling approach in Chapter IV addressed habitat suitability for juvenile mutton snapper in the Gladden Spit area and rest of the Belize shelf. Potential juvenile habitat encompassed 2,408.7 km^2 but only 8.69% of this area was located inside marine protected areas. Using a common spatial framework, Chapter IV illustrated how data on life history, habitat type and distribution, and anthropogenic stressors can be synthesized to guide conservation efforts for Lutjanids in Belize. The spatially discrete model provided a platform for marine spatial planning and management of the Belize shelf, evaluating the degree of protection granted to essential juvenile habitats for snappers, and pinpointing focal areas that deserve special consideration or protection.

In addition to expanding the information available on the biology of mutton snapper, this dissertation contributes to the knowledge of the complex inter-annual and within-season fishery dynamics of their spawning aggregation fisheries, particularly when seen as fisher-fish socio-environmental systems. In particular, this dissertation highlights additional aspects from the mutton snapper fishery at Gladden Spit that need special management consideration. Although Chapter II suggested persistence of the fishery during the last decade of its history, a continued monitoring of annual and monthly trends in CPUE and mutton snapper sizes is warranted. Both monthly and annual CPUE comparisons are needed, given the peculiar inter-annual and within-season variability in catches and fishing effort. Moreover, the baseline and methods developed in this dissertation can be used to detect directional changes in stock status and thus support management of the fishery. However, as mentioned in Chapter II, only a complete stock assessment of the fishery, that includes estimation of age-specific mortality rates and growth parameters, could evaluate the sustainability of the fishery. Chapter III illustrated age-structured mutton snapper spawning aggregations at Gladden Spit and illustrated the high proportion of immature females in June landings. This is important because fecundities of male and female mutton snapper are age specific, as are their fertility rates and the viability of their eggs. Management of mutton snapper fisheries in Belize and rest of the Caribbean needs to consider this biological attribute for projecting population trends and assess future sustainability of the resource.

Though these findings and their implications for the mutton snapper fishery need further investigation, they offer managers essential insights to consider immediately. Results in Chapter III stressed the short term economic gain from June catches compared to the long-term sustainability of the mutton snapper fishery if immature females were released from fishing pressure late in the fishing season. Also, the high number of bycatch species (49) and the high proportion of yellowtail snapper in March landings highlight the need for additional research on the potential economic gains versus losses from fishing impacts to nontarget and unmanaged species early in the season. These results also call for a multi-species approach to fisheries management in Gladden Spit and other multi-species spawning aggregation sites, as opposed to single-species management directed to the most commercially important species (mutton snapper in the time of this dissertation study).

Finally, though the projected distribution of suitable habitat for juvenile mutton snapper in Chapter IV was hypothetical, it illustrated how putative early-life history habitats across the Belize shelf have received less protection from marine protected areas than spawning aggregation sites. Though the relative importance of juvenile versus spawning habitats in the regulation of reef fish populations is an unsolved paradigm and is species and site specific, protected spawning aggregation sites can serve as concentrated sources of eggs and larvae, but unprotected settlement areas and degradation of nursery habitats can detrimentally affect the abundance of future spawners. These results suggest the need for further studies on juvenile habitat requirements and the limitations thereof.

Key to successful long-term, adaptive co-management of the mutton snapper fishery of Gladden Spit is a continued involvement of fishers and other stakeholders in resource monitoring and evaluation, as well as in policy and decision making. The co-management of the fishery is relatively recent in the history of the fishery and this dissertation could only put it into context for further evaluation of its structure and assessment of its efficiency. However, compared to other similar socio-environmental systems, the current co-management arrangement of the artisanal mutton snapper fishery at Gladden Spit has the potential to serve as a platform for cooperation among co-managers, fishers, and rest of stakeholders in resource and market management, monitoring, evaluation, and decision making. This approach is considered key in the management of artisanal coral-reef fisheries and the most viable in rural settings where the food and economic securities of people rely directly on these local marine resources.

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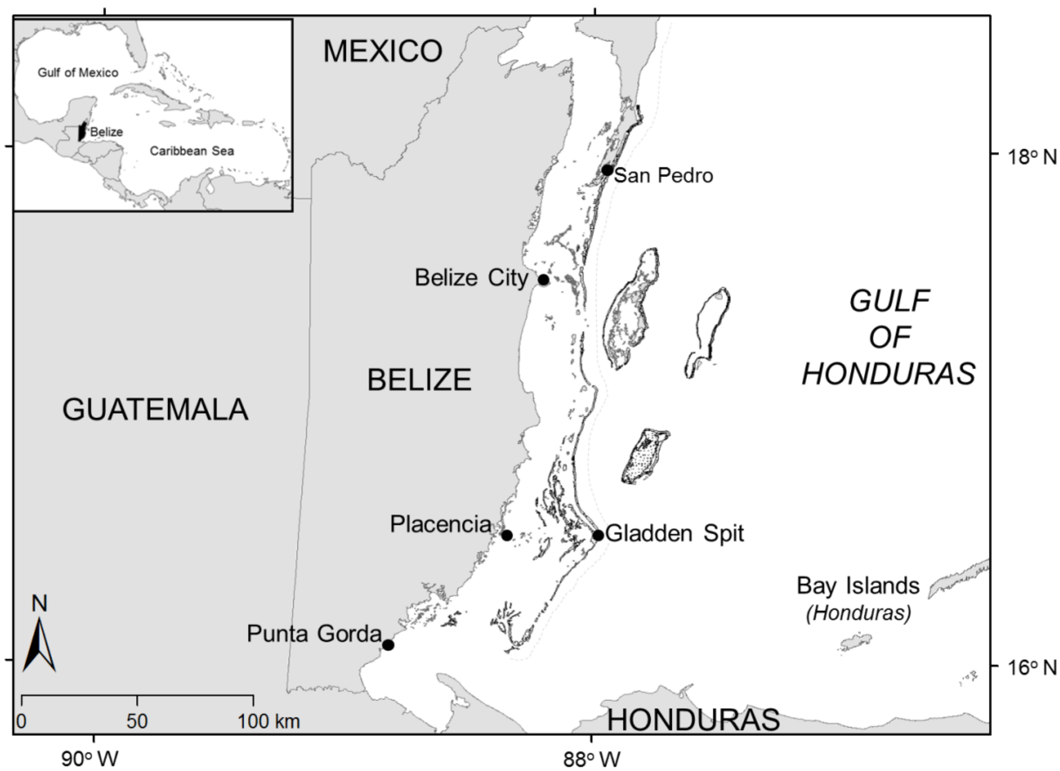
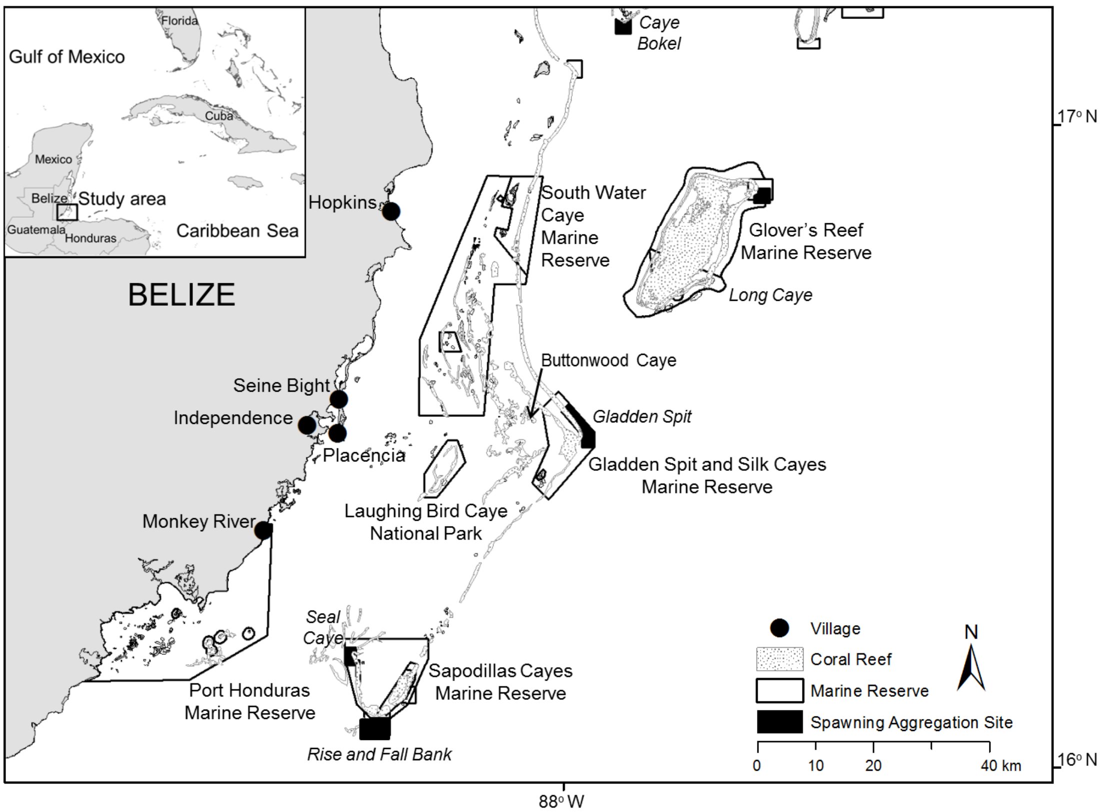
APPENDIX I

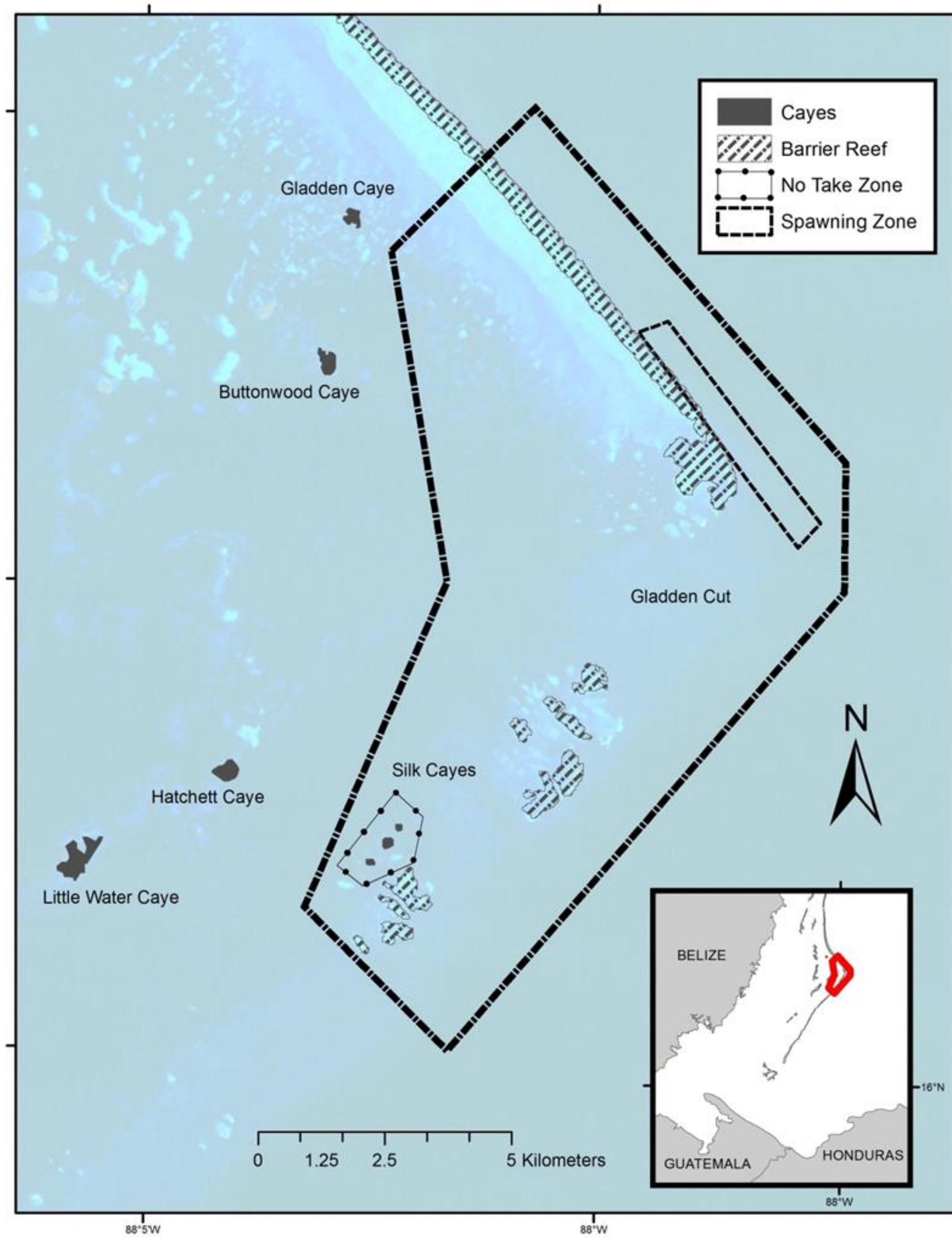
FIGURES



A.1.1. Map of the study area showing the location of Belize as the western boundary of the tri-national Gulf of Honduras, western Caribbean Sea. The southern Mesoamerican Barrier Reef is denoted by a dashed line, east of the Belize coast. Data for GIS themes in map were extracted from Burke and Sugg (2006) and Meerman (2011).



A.1.2. Map of the study area, showing the location of the marine reserves of southern Belize, Buttonwood Caye, and the villages of origin of the fishers from the mutton snapper (*Lutjanus analis*) fishery at Gladden Spit, Belize. The sites where mutton snapper aggregate to spawn along the Barrier Reef (confirmed at Caye Bokel, Long Caye, and Gladden Spit; presumed at Seal Caye and Rise and Fall Bank) are indicated in italics. Data for GIS themes in map were extracted from Burke and Sugg (2006) and Meerman (2011).

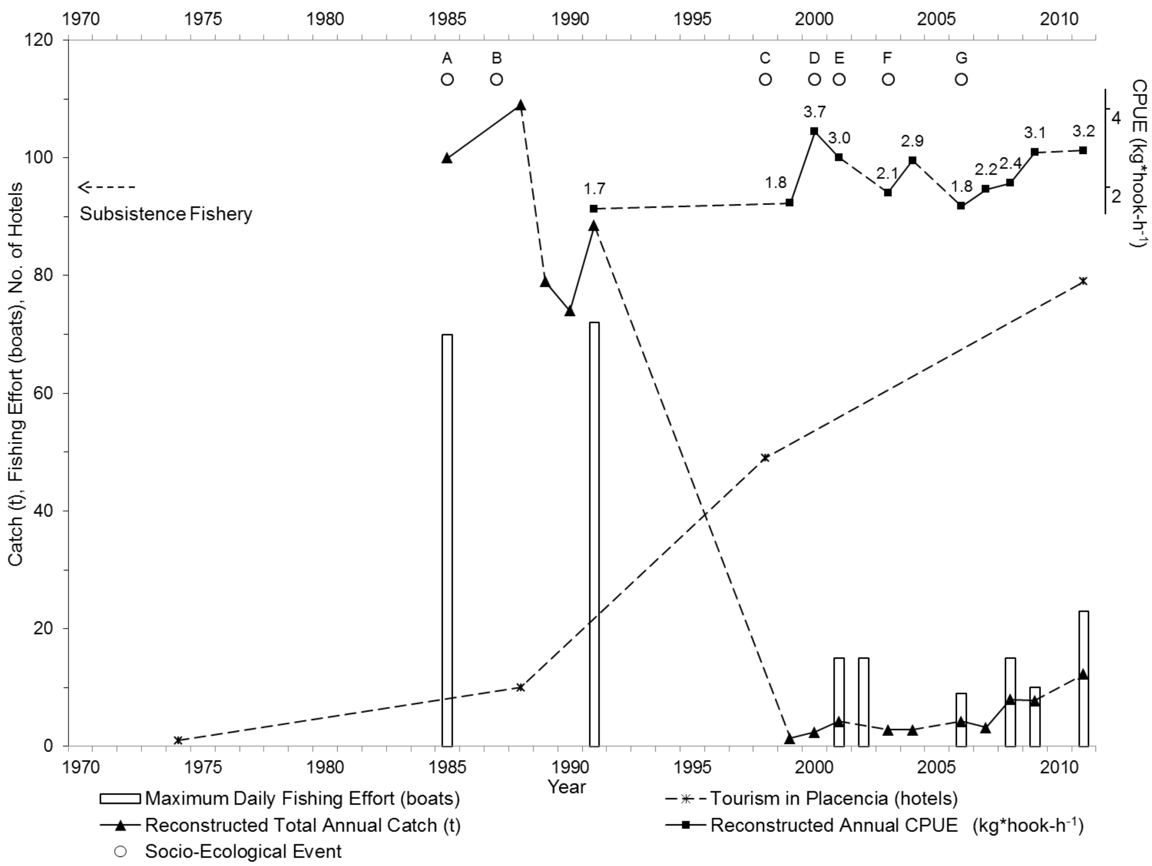


A.1.3. Details of the zoning of the Gladden Spit and Silk Cayes Marine Reserve, Belize, shown in relation to the barrier reef, the shelf edge, and fishing camps at Buttonwood and Gladden Cayes. The No Take Zone and Spawning Zone are encompassed within the multi-use marine reserve.

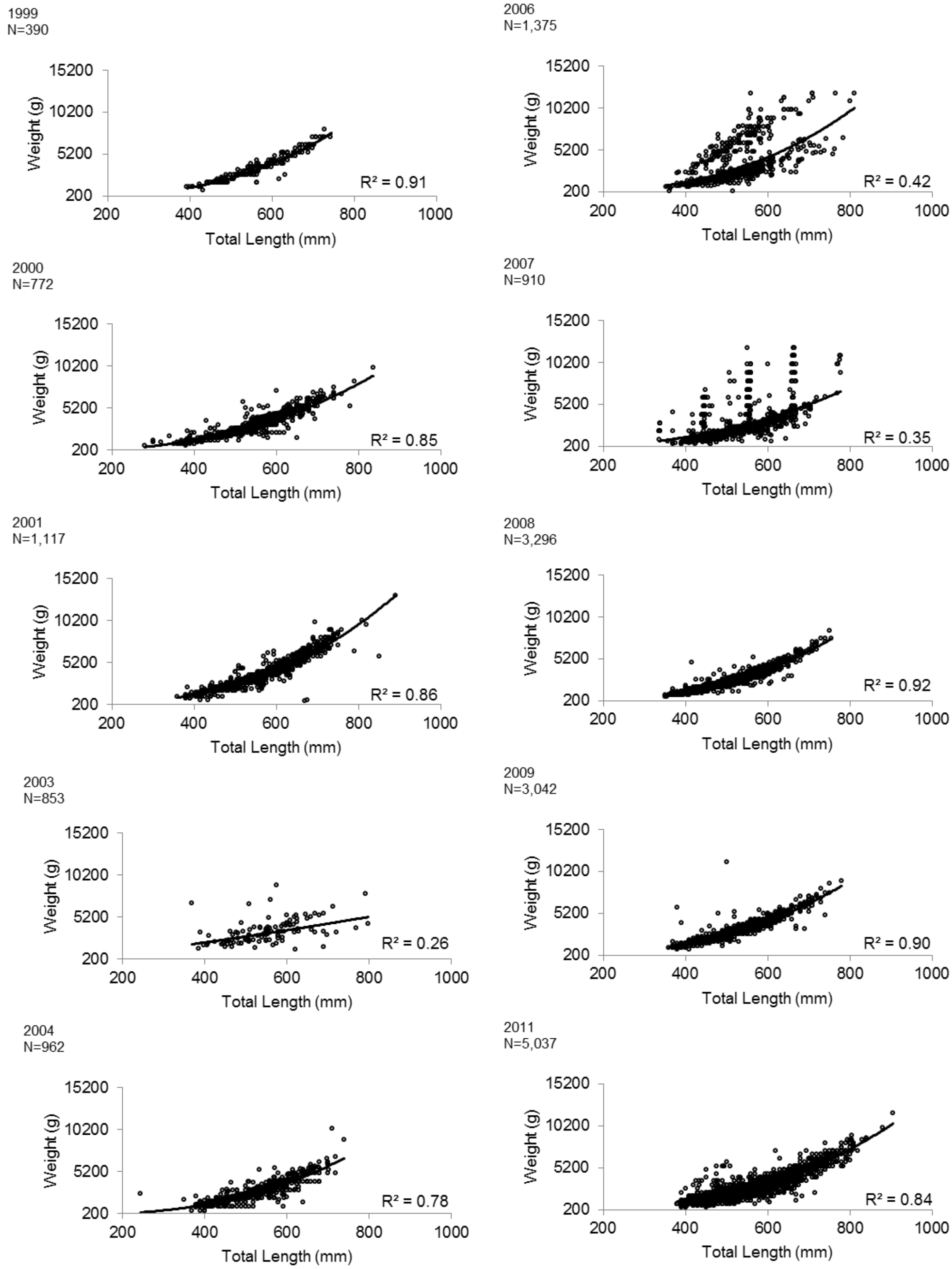
A)

B)

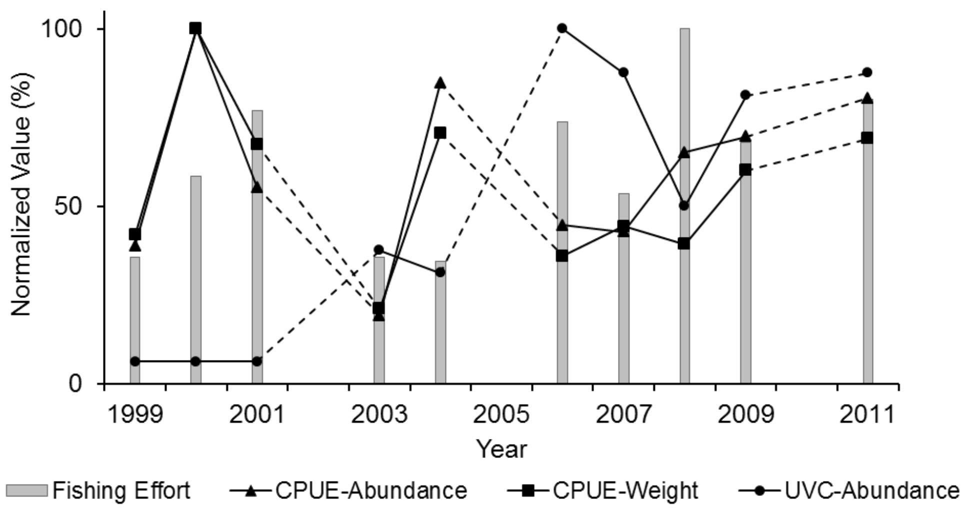
A.1.4. The fishing camp at Buttonwood Caye, Belize in May 2011. (A) The catch is stored in the fishing camp, packed in freshwater ice for 2-3 days before being transported inland for sale. (B) During each day of the fishing season, SEA's landings teams collect fisheries data from the catch.



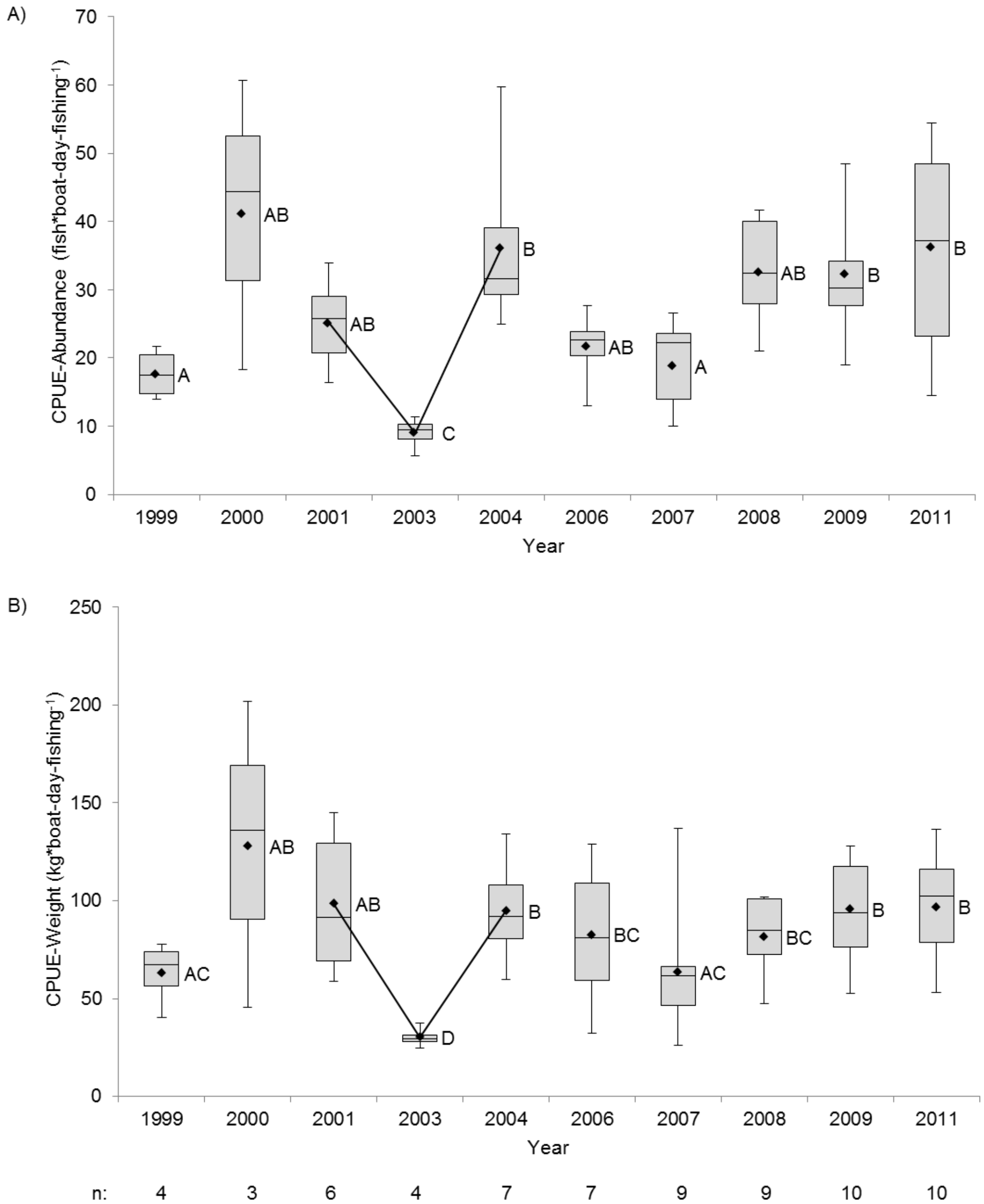
A.1.5. Socio-environmental history (1970-2011) and reconstruction of annual catches (t), daily fishing effort (boats), and catch per unit effort (CPUE, kg*hook-h^{-1}) of the mutton snapper (*Lutjanus analis*) fishery at Gladden Spit, Belize. Tourism development in Placencia is superimposed in the graph. Dashed lines indicate linear projections between years with no data available. Selected socio-economic and management events from Table A.2.2. are plotted (empty circles): (A) start of the expansion of the tourism industry in Belize, (B) shift from the fishing profession to tourism occupations by fishers from Placencia, (C) start of the monitoring of the fish spawning aggregations in Belize, (D) legal declaration of the Gladden Spit and Silk Cayes Marine Reserve, (E) landfall of Hurricane Iris, (F) creation of 11 national marine reserves around fish spawning aggregation sites, (G) enacment of "special licenses" for fishing mutton snapper at Gladden Spit.



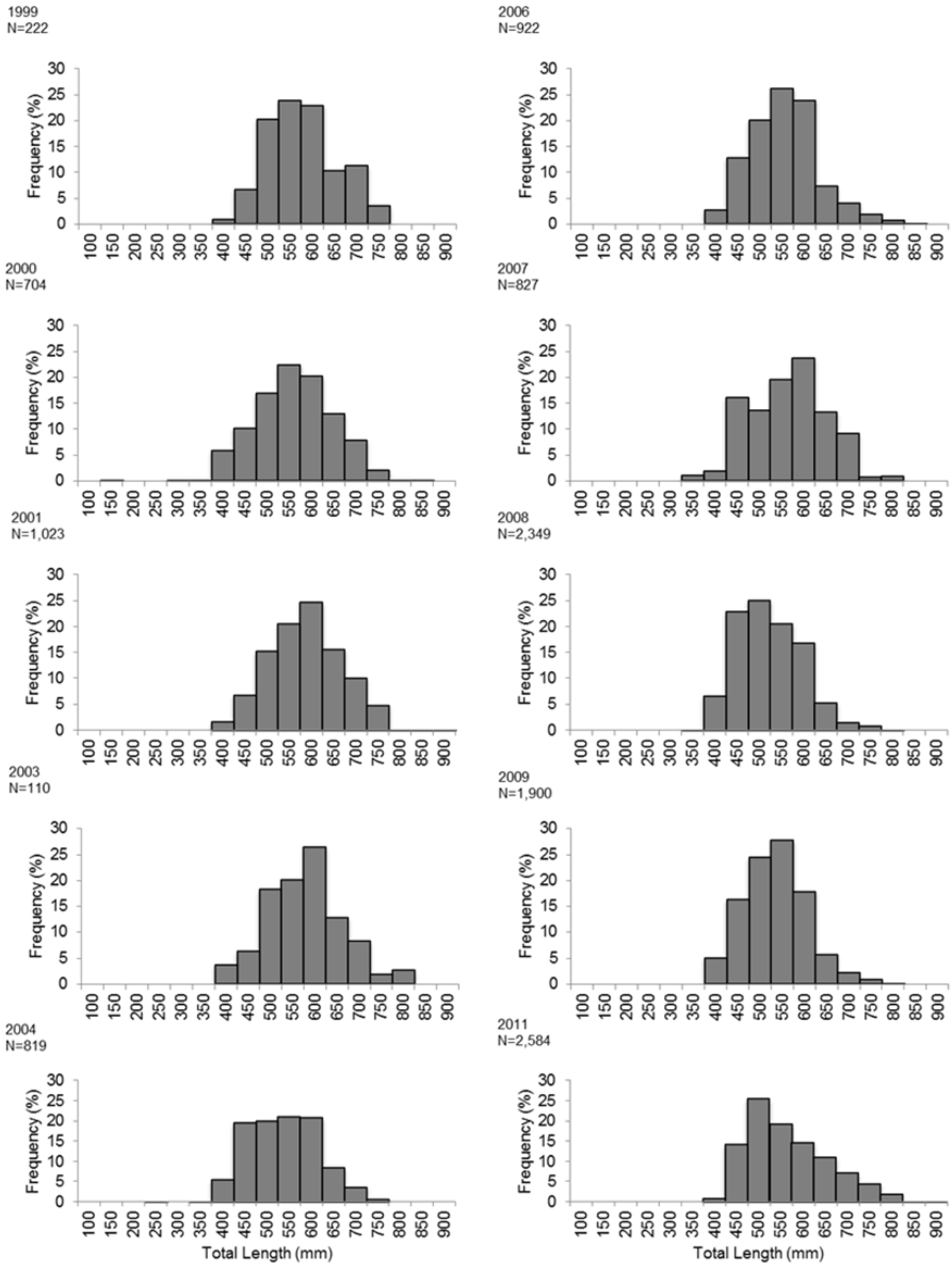
A.1.6. Annual length-weight relationships (1999-2011) of mutton snapper (*Lutjanus analis*) landed at Buttonwood Caye, Belize. Deviations from the expected power model ($R^2 < 0.50$) in 2003, 2006, and 2007 are artifacts of sample size and replacement of data-collection teams during landings surveys.



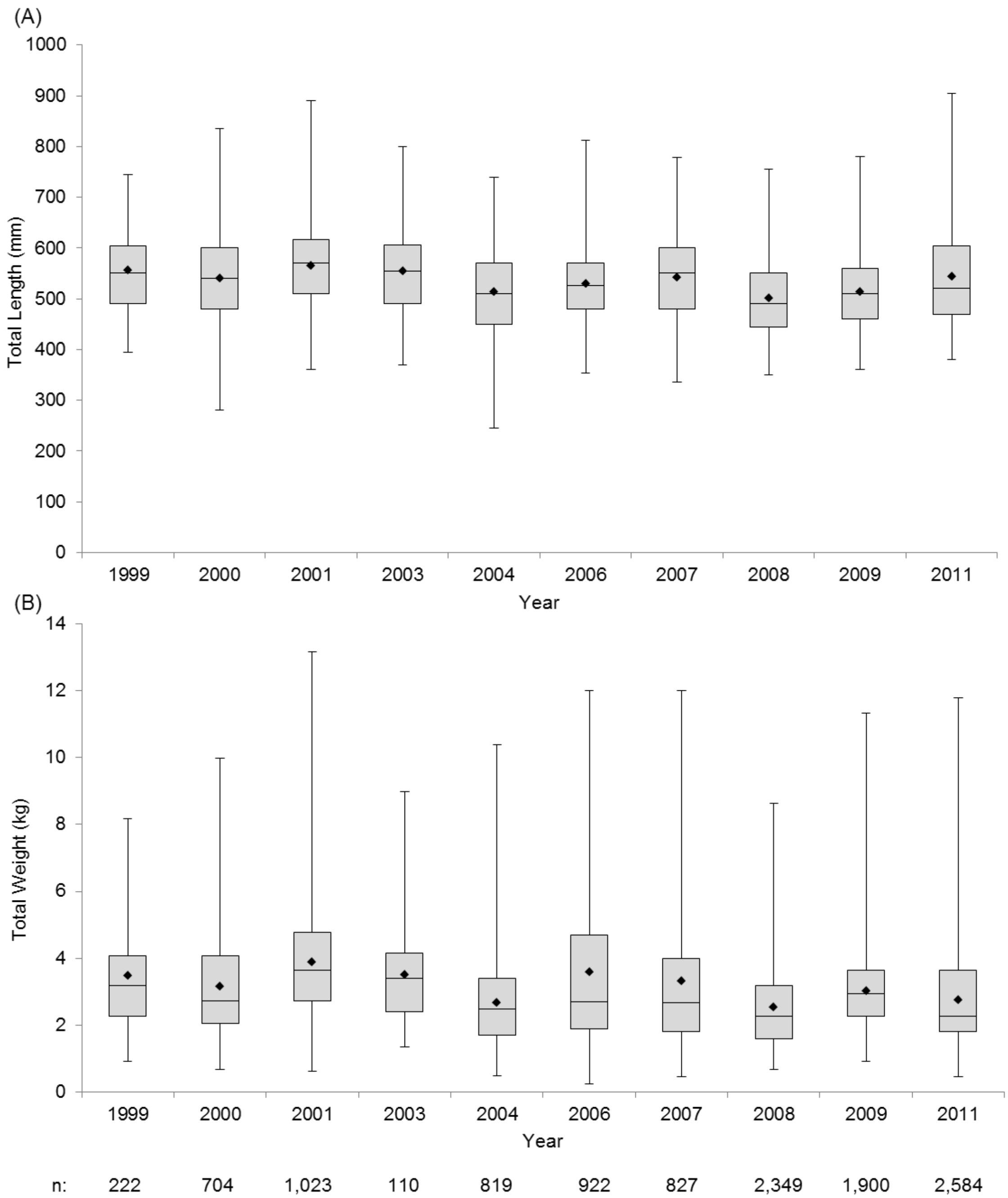
A.1.7. Inter-annual trends (1999-2011) in annual fishing effort, catch per unit effort in numbers (CPUE-Abundance) and weight (CPUE-Weight), and peak underwater visual census counts (UVC-Abundance) of mutton snapper (*Lutjanus analis*) at Gladden Spit, Belize. Variables were normalized to the maximum annual value and graphed as ratios (%) for comparison purposes. Dashed lines or absent bars in the graph indicate that there were no data available for the year.



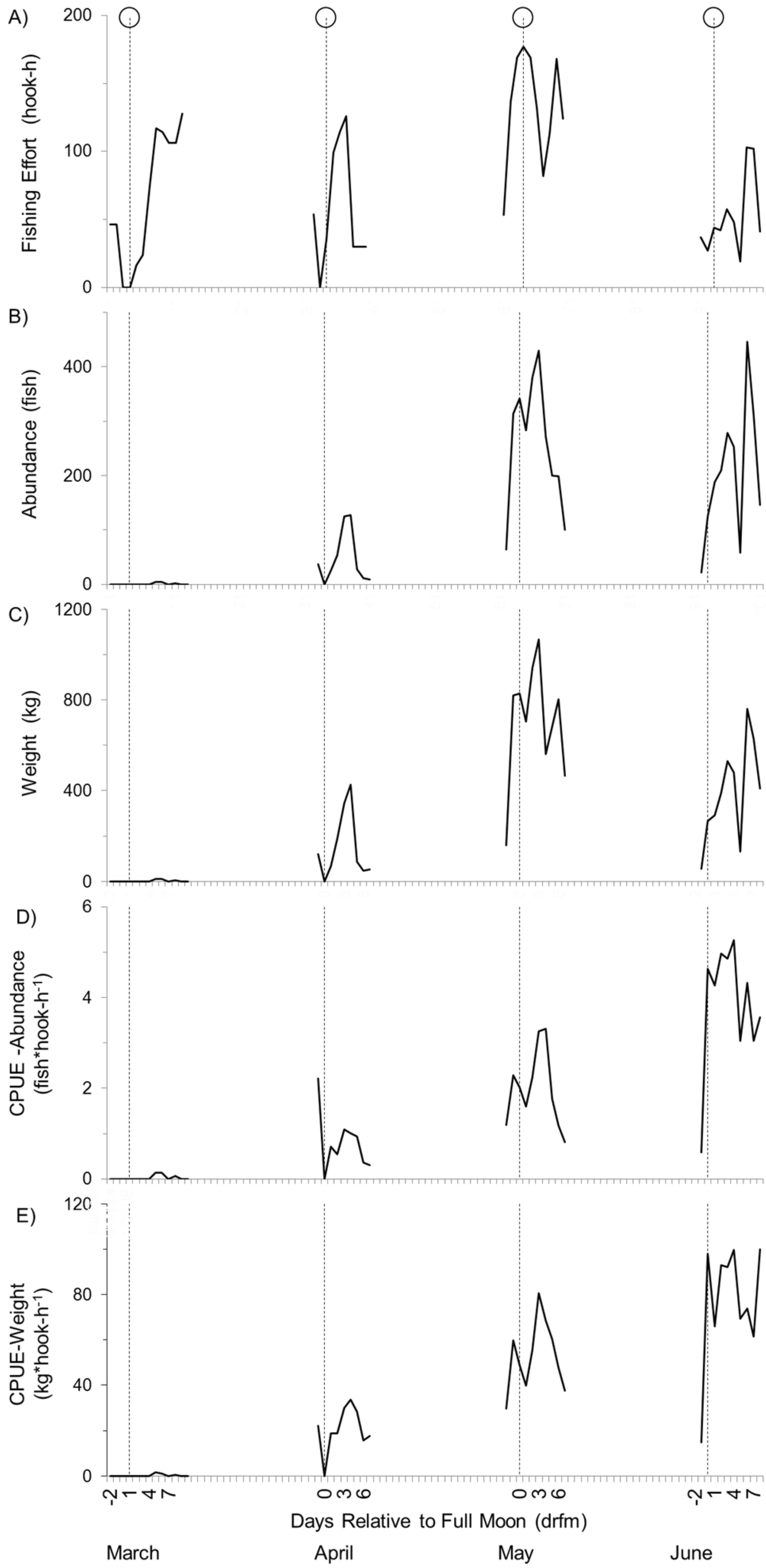
A.1.8. Inter-annual trends (1999-2011) in daily estimates of catch per unit effort (CPUE) by (A) numbers (CPUE-Abundance, fish*boat-day-fishing^{-1}) and (B) weight (CPUE-Weight, kg*boat-day-fishing^{-1}) of mutton snapper (*Lutjanus analis*) landed in May at Buttonwood Caye, Belize. Means are denoted by diamonds (♦) in whisker box plots. Annual changes in CPUE estimates were tested using PERMANOVA routines (one-way PERMANOVAs: df=9 and 59; α=0.05). Posterior pair-wise testing of significant means is based on 9,999 permutations and significant changes between successive years are indicated by solid lines ($p \leq 0.05$). The lack of at least one letter in common (i.e., A, B, C, and D) indicates significantly different means between any pair of years.



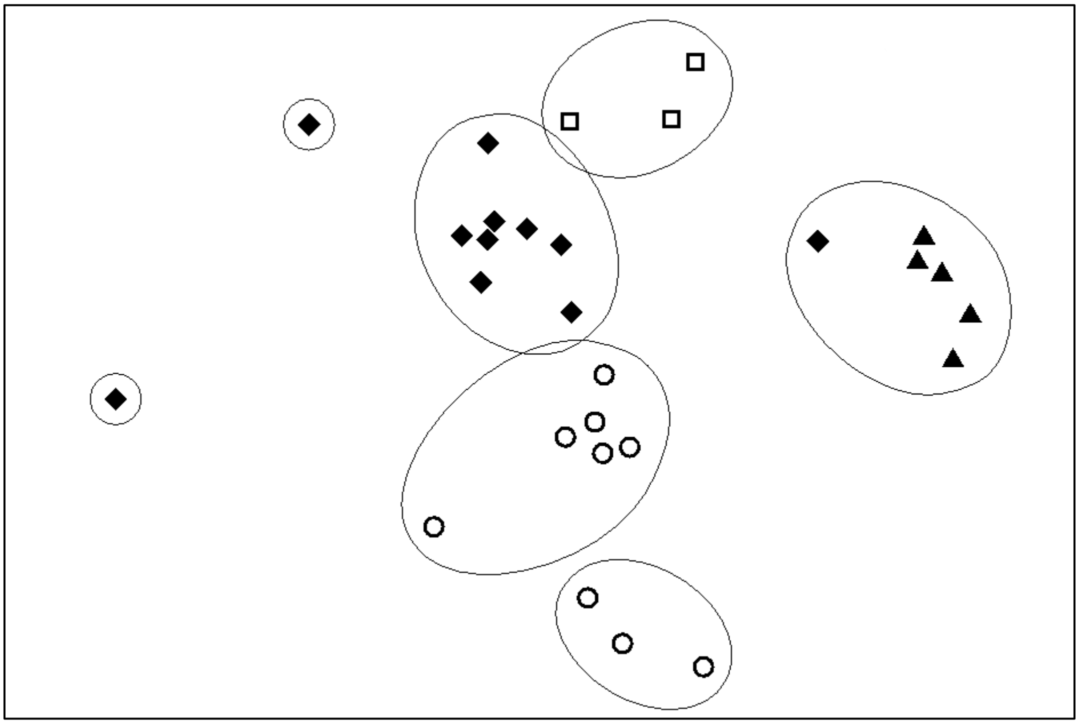
A.1.9. Annual length-frequency distributions (1999-2011) of mutton snapper (*Lutjanus analis*) landed in May at Buttonwood Caye, Belize.



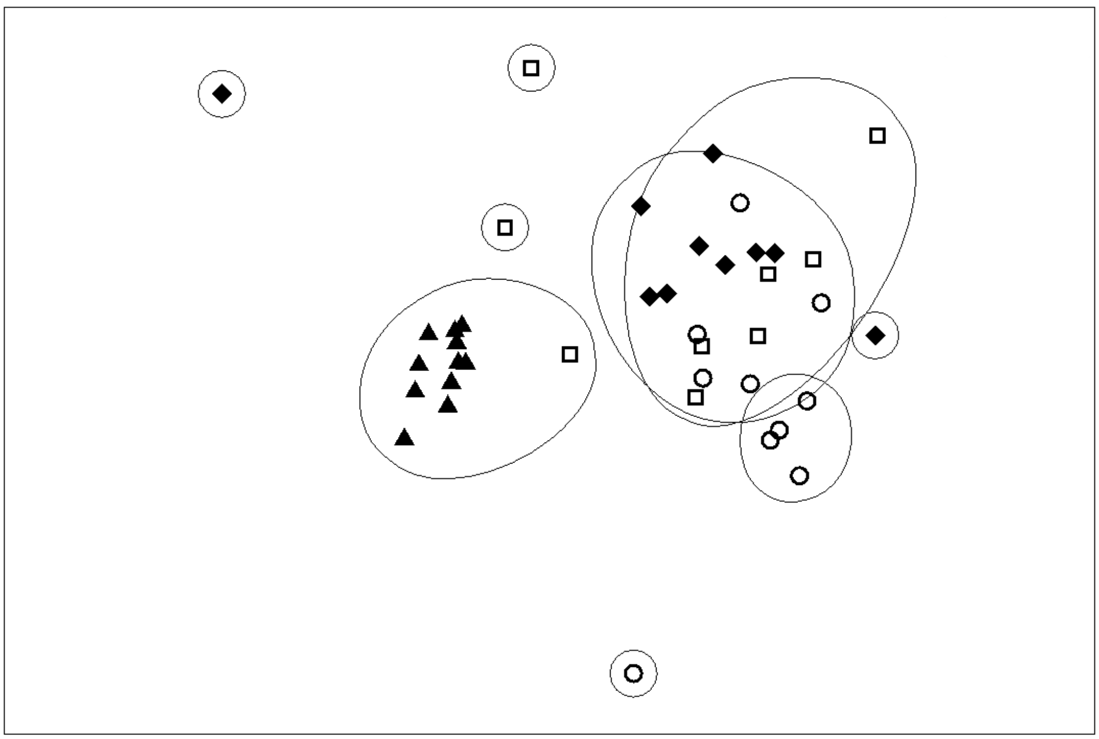
A.1.10. Inter-annual trends (1999-2011) in (A) individual total length (mm) and (B) individual total weight (kg) of mutton snapper (*Lutjanus analis*) landed in May at Buttonwood Caye, Belize. Means are denoted by diamonds (♦) in whisker box plots. No significant changes among years were detected in individual median lengths or weights (one-way PERMANOVAs: pseudo-F≤1.9, df=9 and 59, p≥0.10).



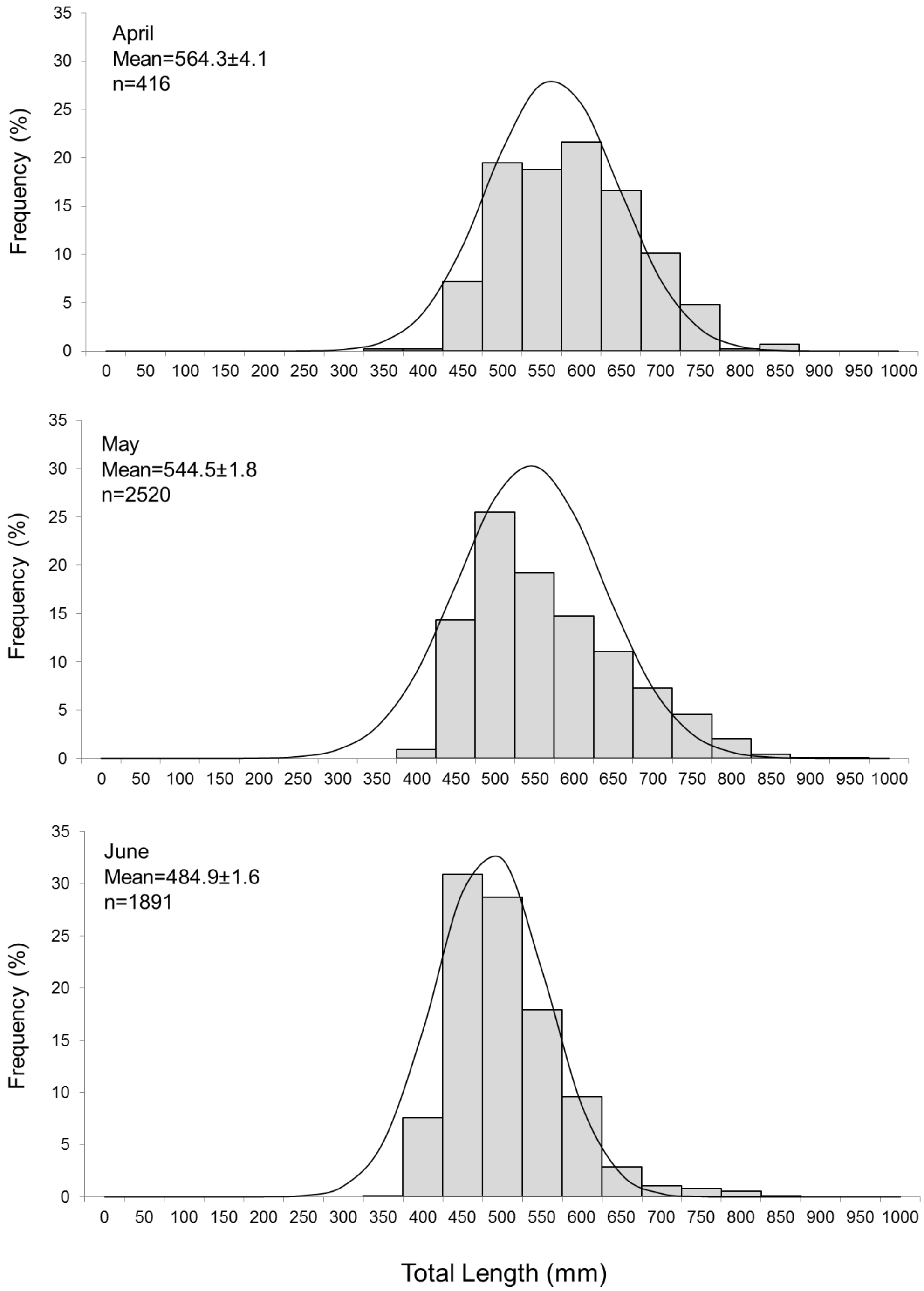
A.1.11. Daily trends in (A) fishing effort (hook-h^{-1}), (B) catch abundance (fish), (C) catch weight (kg), (D) CPUE-Abundance (fish* hook-h^{-1}), and (E) CPUE-Weight (kg* hook-h^{-1}) estimated from mutton snapper (*Lutjanus analis*) landings at Buttonwood Caye, Belize, between March and June 2011. Variables are plotted against time, -1 to 7 drfm (days relative to full moon). Open circles indicate days of full moon with dates March 19, April 17, May 17, and June 15.



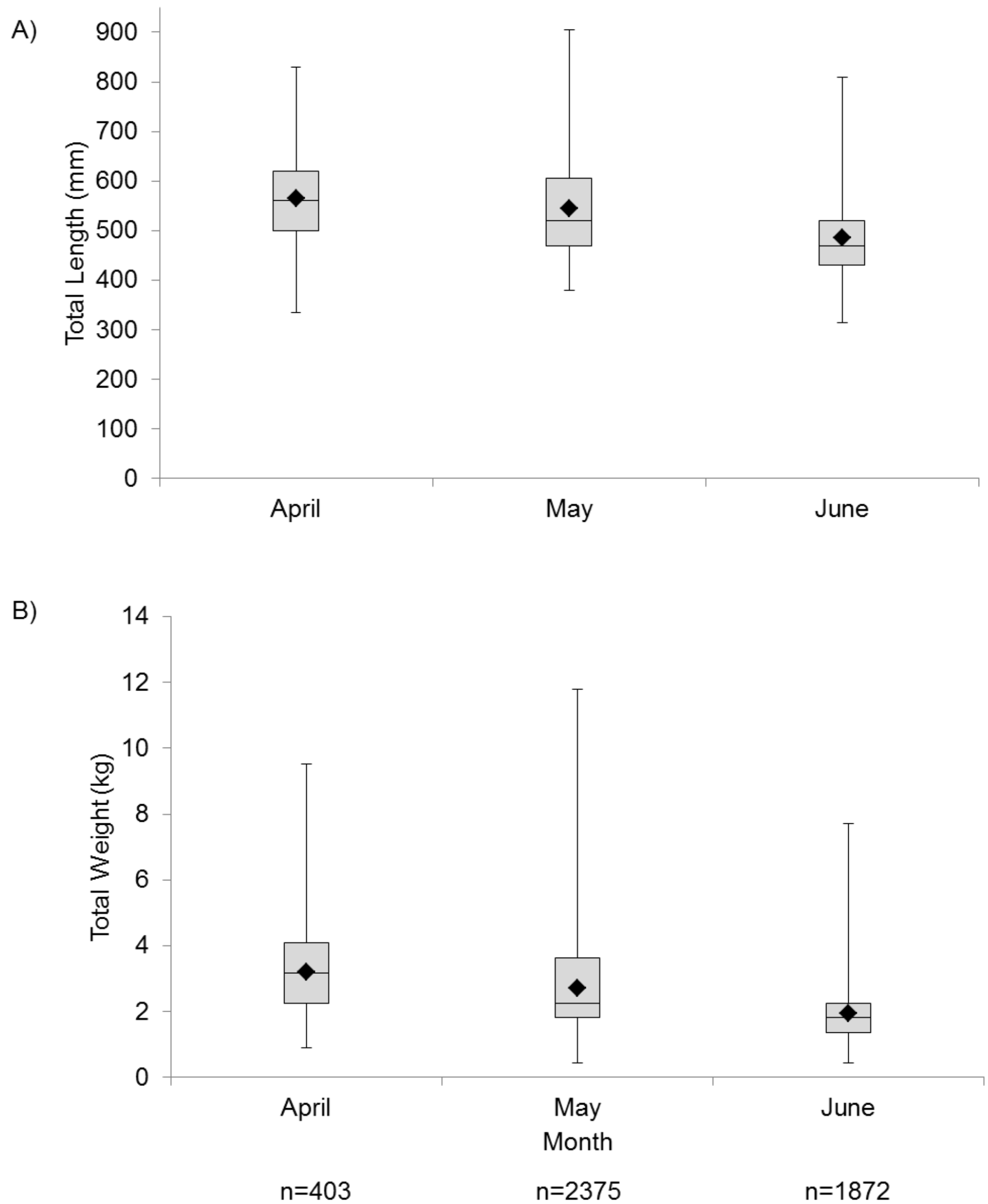
A.1.12. Non-metric multidimensional scaling (NMDS) plot (2-dimensional stress=0.17) of the fleet composition (boats) of the mutton snapper (*Lutjanus analis*) fishery at Gladden Spit, Belize, during the 2011 fishing season. The NMDS configuration was ordered by month (March ▲, April □, May ♦, and June ○) and group-averaged clustering from Bray-Curtis similarities were superimposed at similarities of 50%.



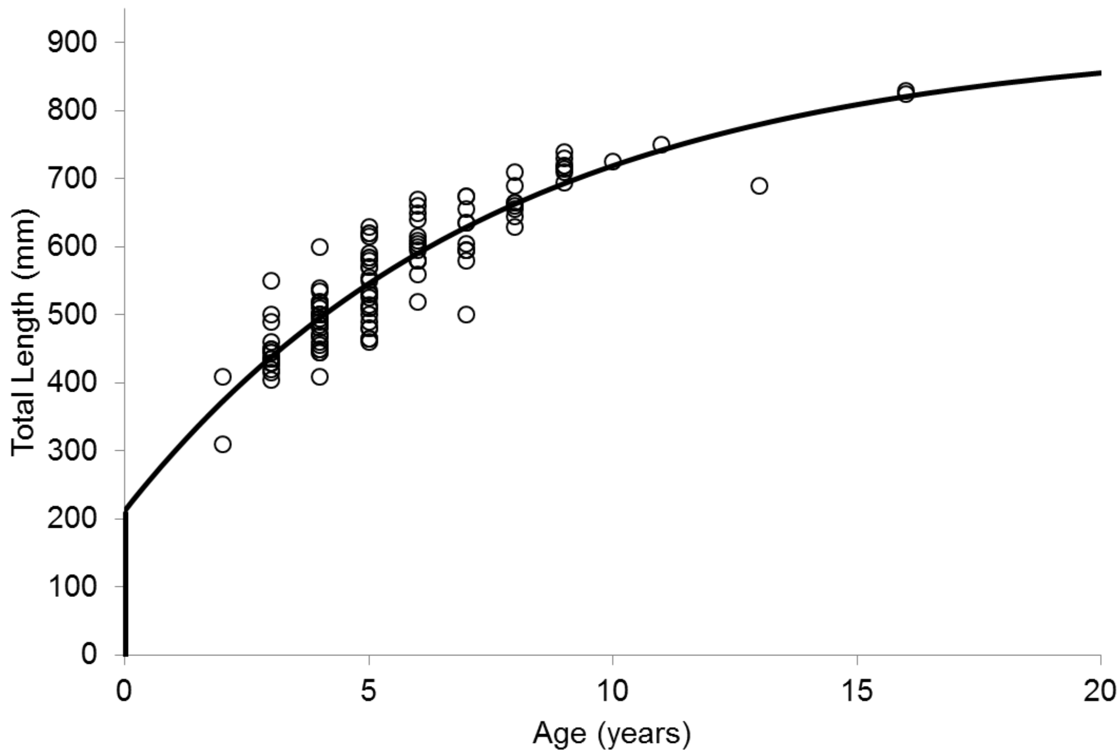
A.1.13. Non-metric multidimensional scaling (NMDS) plot (2-dimensional stress=0.14) of the bycatch composition (species) of the mutton snapper (*Lutjanus analis*) fishery at Gladden Spit, Belize, during the 2011 fishing season. The NMDS configuration was ordered by month (March ▲, April □, May ♦, and June ○) and group-averaged clustering from Bray-Curtis similarities were superimposed at similarities of 50%.



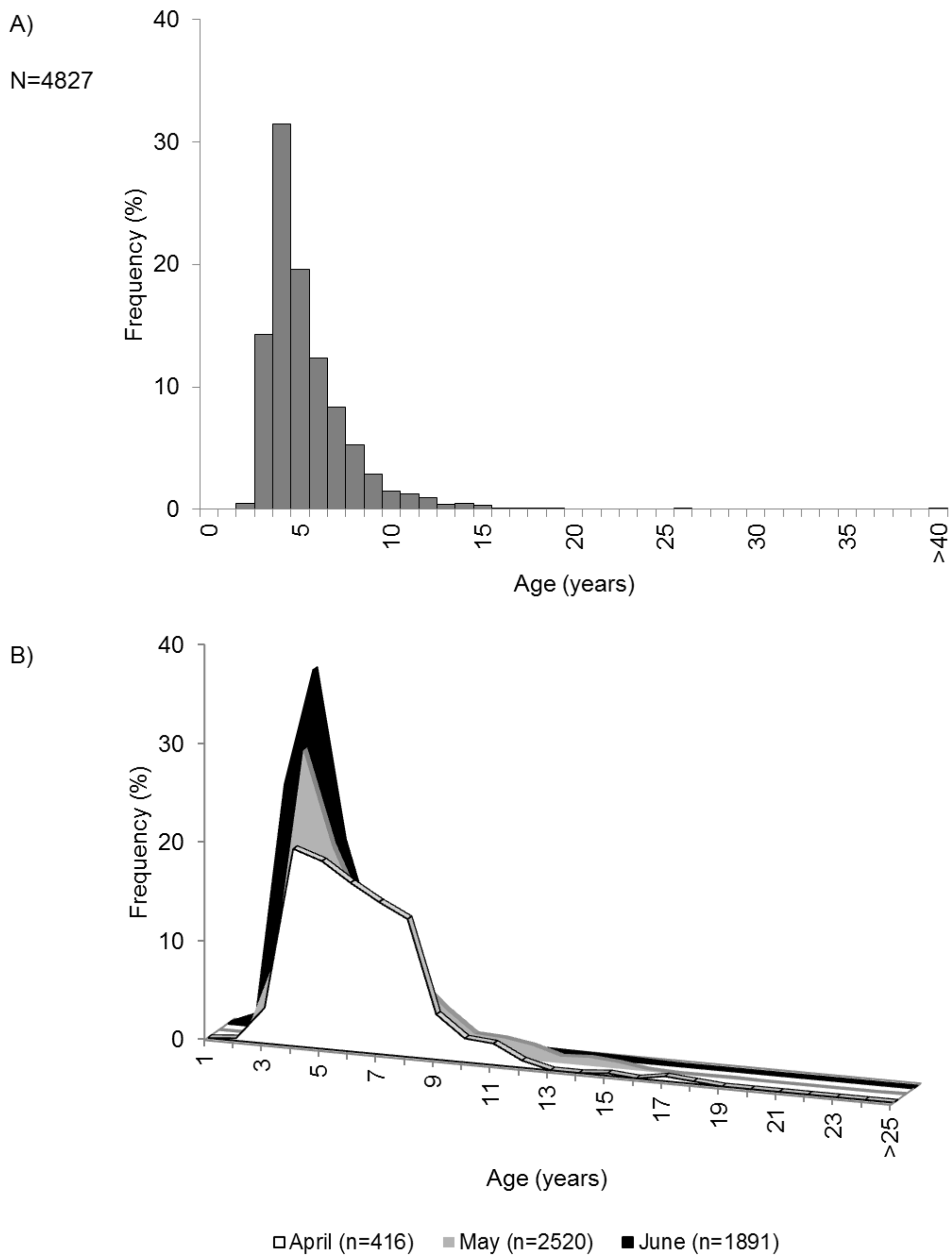
A.1.14. Length-frequency distributions of mutton snapper (*Lutjanus analis*) landed at Buttonwood Caye, Belize, between April and June 2011. Female and male data are combined in histograms. Mean sizes (±SE) and sample sizes (n) are included.



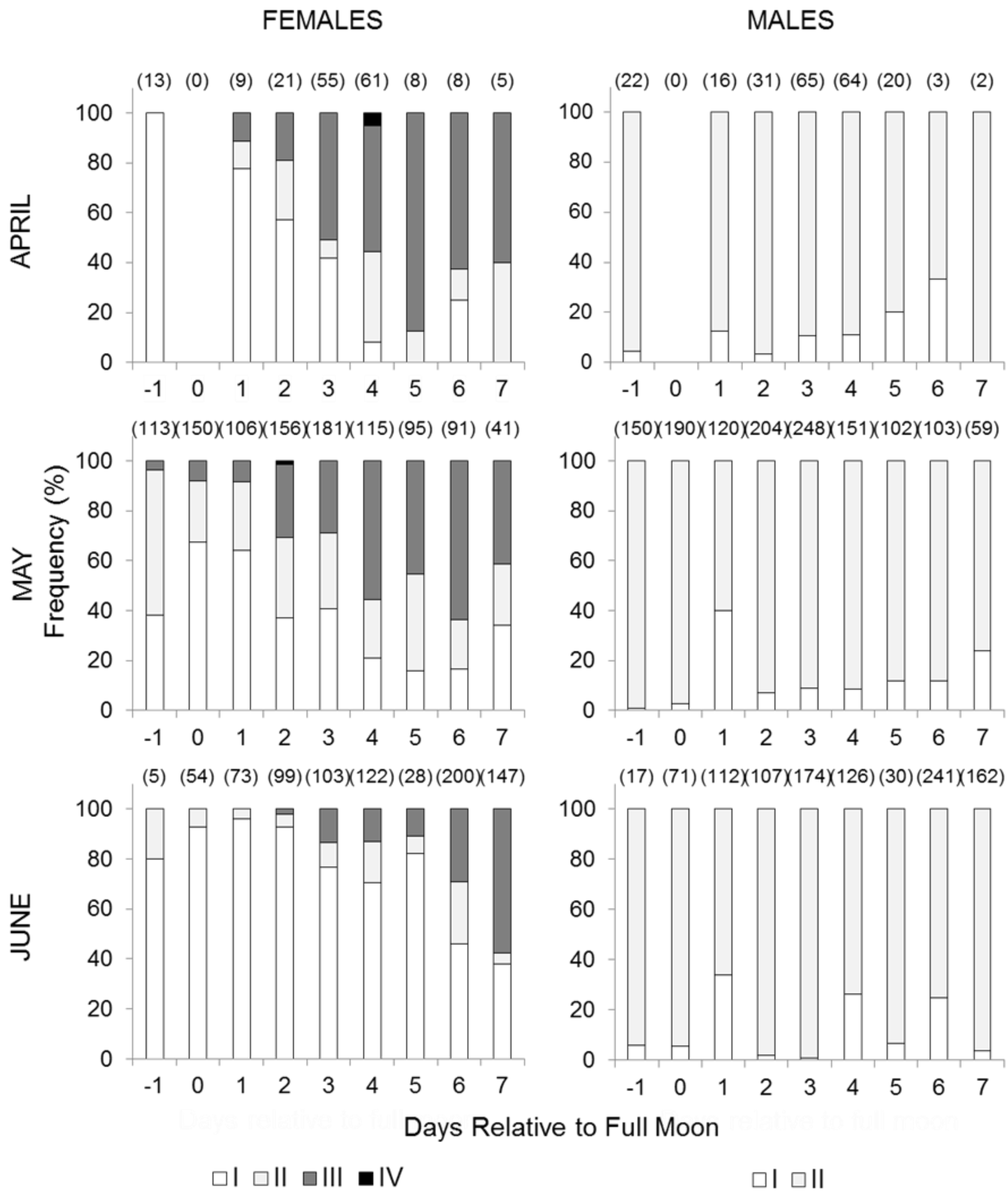
A.1.15. Monthly trends (April-June) in (A) individual length (mm) and (B) individual weight (kg) of mutton snapper (*Lutjanus analis*) landed at Buttonwood Caye, Belize, between April and June 2011. Means are denoted by diamonds (♦) in whisker box plots. Individual TL and TW varied significantly among months (one-way PERMANOVAs: pseudo-F>14.1, df=2 and 24, p<0.0001) and were particularly smaller in June (posterior-PERMANOVA pair-wise tests: p<0.007).



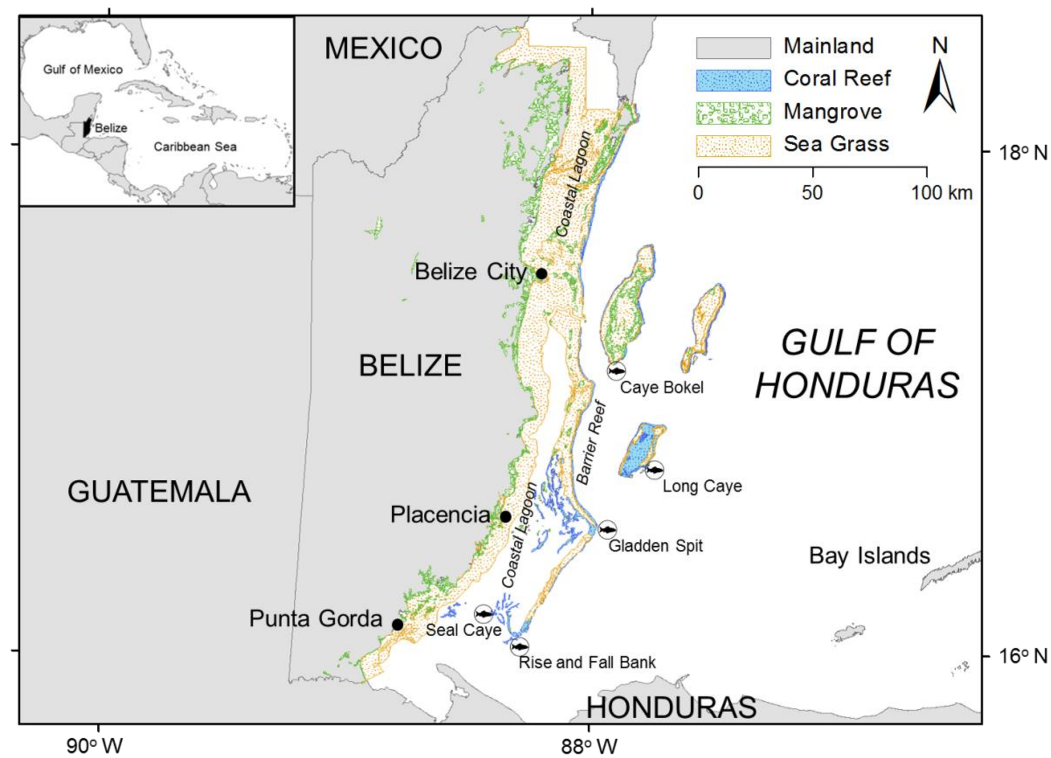
A.1.16. Observed (scattered points) and theoretical total lengths (TL, mm) at age (years) of mutton snapper (*Lutjanus analis*) landed at Buttonwood Caye, Belize, between April and June 2011. The von Bertalanffy growth equation ($L_t=L_\infty*(1-e^{-k(t-to)})$, where L_t is TL (mm) at age t (years), L_∞ the mean asymptotic TL, K the Brody growth coefficient, and t_o the hypothetical age at which the fish would have 0 mm TL) that best fitted the observed data was $TL=905.95*(1-e^{-0.13(t-(-2.04))})$ (R^2=0.82, MSE=$1.79*10^{-3}$, n=115).



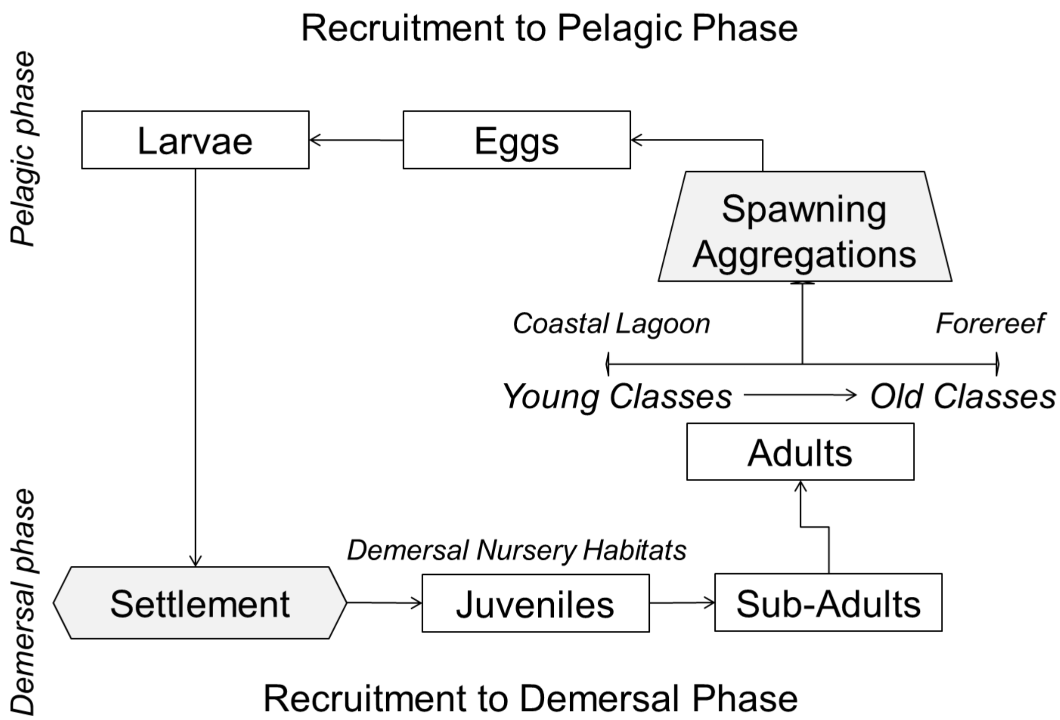
A.1.17. Annual (A) and monthly (B) age-frequency distributions of mutton snapper (*Lutjanus analis*) landed at Buttonwood Caye, Belize, between April and June 2011. Distribution of individuals in age classes varied among month (one-way PERMANOVAs: pseudo-F=11.4, df=8 and 18, p=0.0005), with individuals significantly younger in June (posterior-PERMANOVA pair-wise tests: p<0.0003).



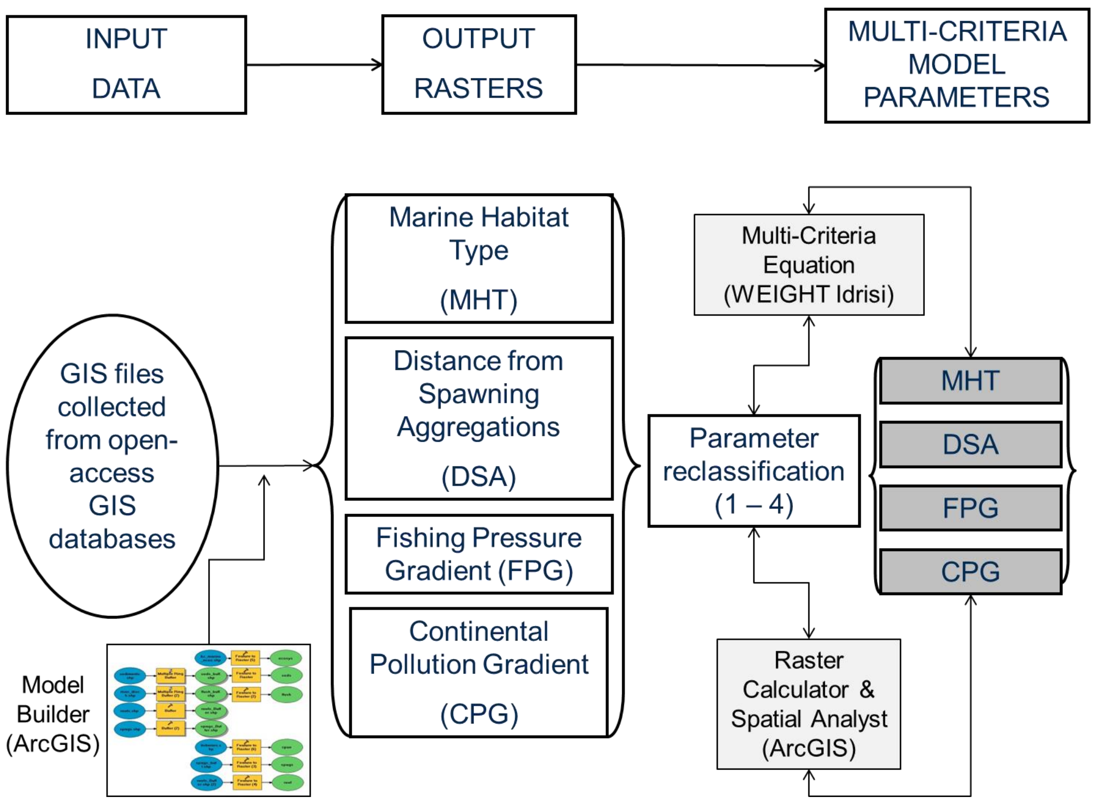
A.1.18. Percentage of female (left) and male (right) mutton snapper (*Lutjanus analis*) in each gonad state (Type I-IV for females; Type I-II for males) determined between April and June 2011 at Buttonwood Caye, Belize. Gonad state was determined macroscopically, with mature individuals with gonads in Type II or beyond. Gonad state types are represented by different shading in bars (legends at bottom of the figure). Sample sizes (n) are indicated above bars.



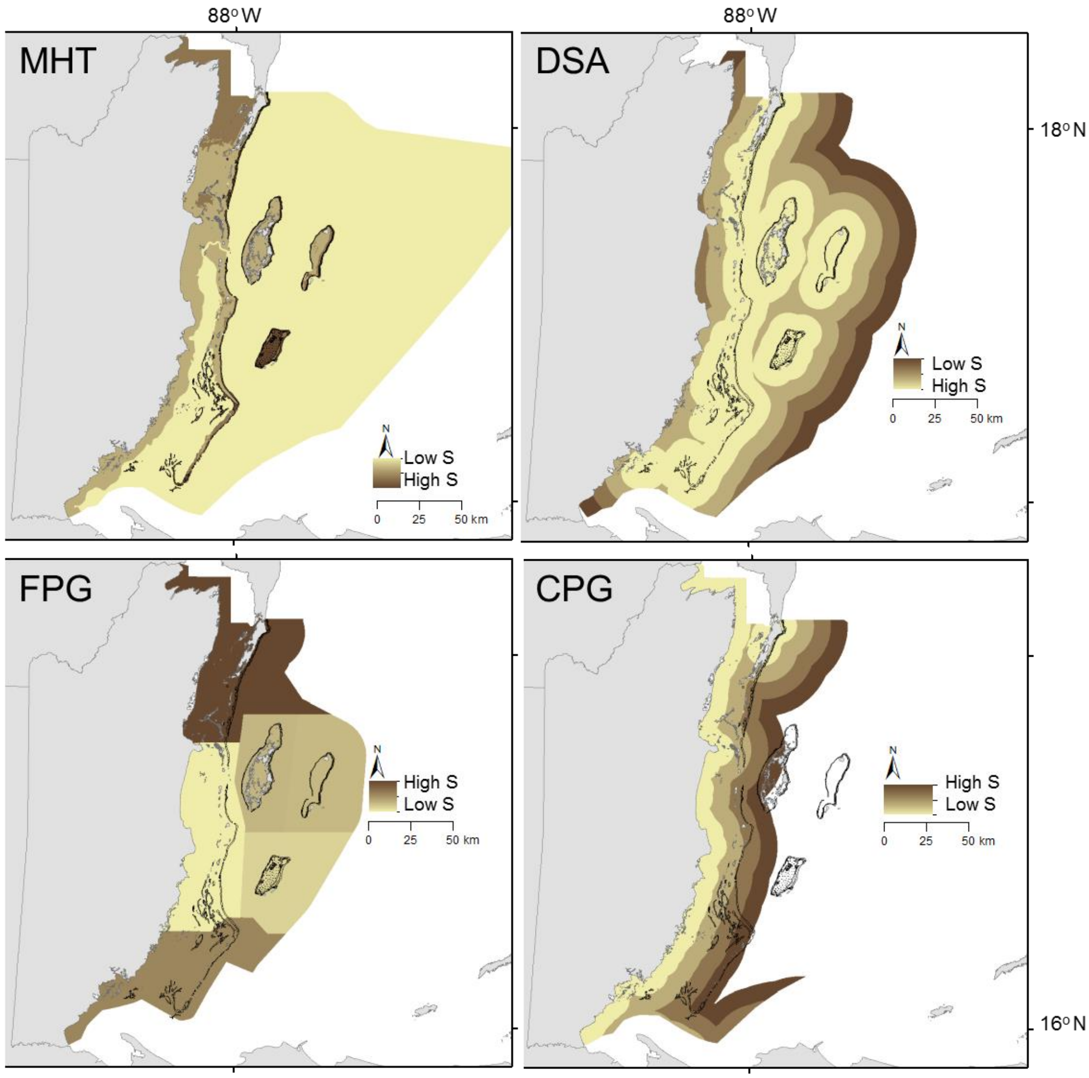
A.1.19. Map of the study area, showing the location of the major marine habitats of the Belize shelf (coastal lagoon and barrier reef), west of the Gulf of Honduras. The sites where mutton snapper (*Lutjanus analis*) aggregate to spawn along the shelf (confirmed at Caye Bokel, Long Caye, and Gladden Spit; presumed at Seal Caye and Rise and Fall Bank) are marked with fish symbols. GIS themes for this map were extracted from Burke and Sugg (2006) and Meerman (2011).



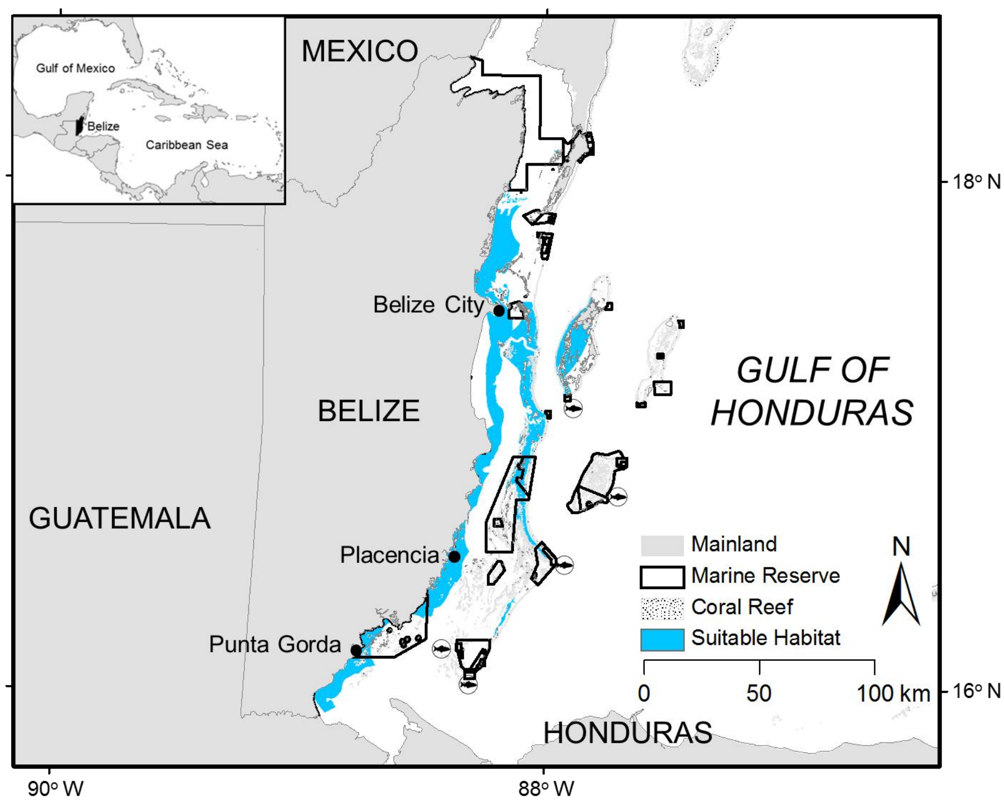
A.1.20. Diagram of the life cycle of mutton snapper (*Lutjanus analis*). The pelagic and demersal phases are coupled when demersal adults spawn pelagic eggs, and when larval survivors or pelagic juveniles recruit into demersal nursery habitats. Recruitment of survivals to the demersal and pelagic phases is highly variable.



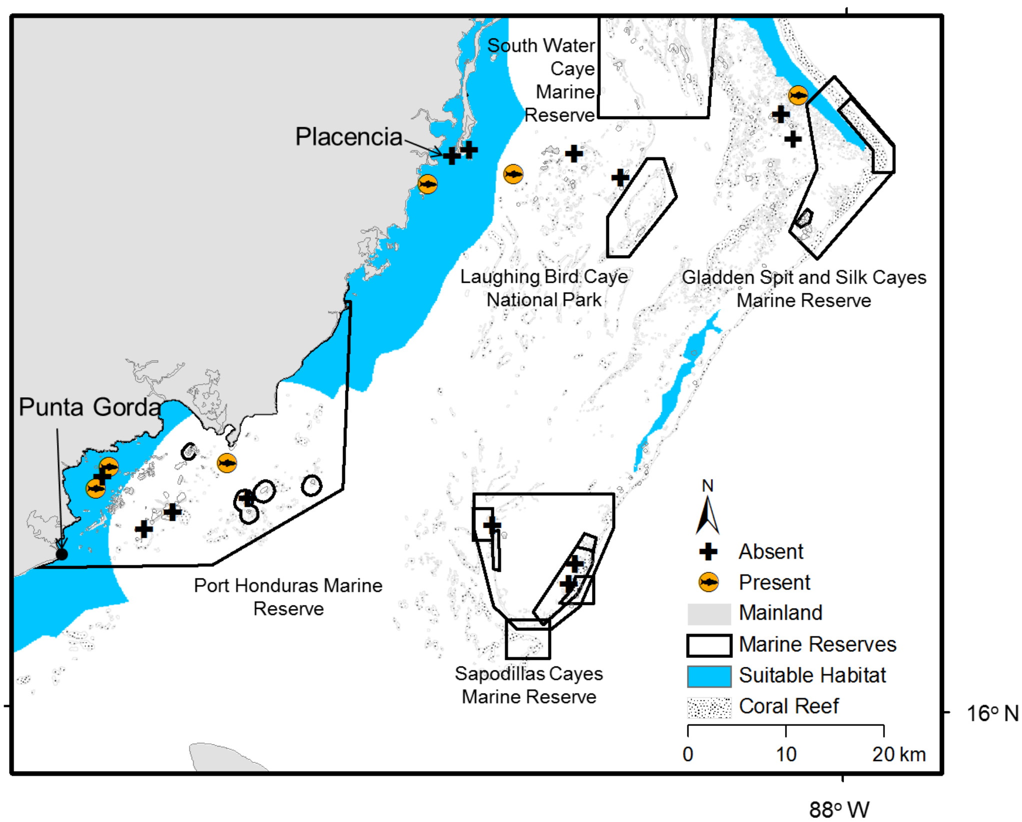
A.1.21. Conceptual GIS-based weighted multi-criteria model for projecting suitable habitat for juvenile mutton snapper (*Lutjanus analis*) across the Belize shelf. ArcGIS was used for geoprocessing and parameterizing the model. IDRISI-Andes was used for geostatistically processing the weighted linear combination function for determining habitat suitability (S). Mathematically, $S= \Sigma (w_i*x_i)$, where (i) is a parameter considered in the spatial model, (w) a weight assigned to parameter (i) based on the model assumptions, and (x) a geostatistically-corrected correlation weight (Eigen value) for parameter (i).



A.1.22. Spatial representation of the weighted parameters used in the GIS-based weighted multi-criteria evaluation function for projecting habitat suitability of juvenile mutton snapper (*Lutjanus analis*) across the Belize shelf. Marine habitat type (MHT), distance from spawning aggregation sites (DSA), fishing pressure gradient (FPG), and continental pollution gradient (CPG) were the four parameters (i) that determined habitat suitability (S). Weights were assigned to each parameter based on the assumptions of the model and ranged from 1 (low S) to 4 (high S).



A.1.23. Map of the projected suitable habitat for juvenile mutton snapper (*Lutjanus analis*) across the Belize shelf. The weighted linear combination function describing the distribution of the projected suitable habitat is
S = 0.56*(MHT) + 0.27*(DSA) + 0.10*(CPG) + 0.07*(FPG), where MHT denotes marine habitat type, DSA distance from spawning aggregation sites, CPG continental pollution gradient, and FPG fishing pressure gradient. Only 8.69% of the projected suitable habitat is located inside marine protected areas.



A.1.24. Evaluation of the GIS-based model of habitat suitability for juvenile mutton snapper (*Lutjanus analis*) across the southern Belize shelf. A total of 648 underwater visual census (UVC) belt transects were conducted in March and July 2009. UVC transects were distributed among 18 sampling stations to determine presence-absence of juvenile mutton snapper (*Lutjanus analis*) across the southern Belize shelf. Presence of mutton snapper in sampling stations is denoted by fish symbols (n=6), absence by crosses (n=12).

APPENDIX II

TABLES

A.2.1. Monthly and annual allocation (1999-2011) of sampling effort (n = survey days) of the mutton snapper (*Lutjanus analis*) landings surveys conducted at Buttonwood Caye, Belize. Landings surveys were conducted by The Nature Conservancy and the Belize Fisheries Department (BFD) between 1999 and 2004 and by Friends of Nature/Southern Environmental Association (SEA) and the BFD between 2006 and 2011. Surveys were not conducted in 2005 and 2010. Data were missing from SEA's database for 2002. Missing monthly surveys are denoted by dashes (-).

Time Period	1999	2000	2001	2003	2004	2006	2007	2008	2009	2011
March	-	1	-	-	-	-	-	-	-	13
April	-	3	4	9	6	6	-	8	6	11
May	4	3	6	4	7	7	9	9	10	10
June	3	-	-	-	-	8	1	7	5	11
Year	7	7	10	13	13	21	10	24	21	45

A.2.2. Socio-environmental timeline in the history of the artisanal mutton snapper (*Lutjanus analis*) fishery at Gladden Spit, Belize. The list was created with information from several sources (Craig, 1966; FAO, 1968; Shusterich, 1984; King, 1997; Vellos, 2001; Key, 2002; Gibson et al., 2004; Goetze, 2005; Huitric, 2005; Gray, 2009; FAO, 2010; Heyman, 2011; Heyman and Granados-Dieseldorff, 2012; Belize Airports Authority, personal communication).

Year	Socio-Ecological Event
1936	Placencia was formally established as a fishing village on the peninsula
1950	Foreign-financed freezing plants opened in British Honduras and initiated lobster export
1952	National lobster exports spiked for the first time since 1920s
1961	Hurricane Hattie (Category 5) destroyed Seine Bight and severely impacted British Honduras
1962	Placencia Cooperative Society Ltd. (Placencia Cooperative) was created
	National production and export of lobster and conch fisheries increase
1965	National lobster exports spiked again
1970	Placencia Cooperative began to generate electricity and produce ice to support the fishing industry
1974	First hotel was built in Placencia (Rum Point Inn)
1975	National conch production peaked for the first time since the 1950s
1976	National conch production declined back to former levels
1979	Placencia gravel airstrip was in service
1981	British Honduras gained independence from Great Britain and re-named Belize
	National lobster production peaked and exports spiked again
1982	Motorized Mexican-style skiffs were introduced in Placencia
1984	Illegal fishing and foreign poaching began to proliferate in southern Belize
1985	National lobster and conch production showed precipitous decline
	Tourism development began to expand rapidly in Belize
1986	Dirt road reaches Placencia Village for the first time
1987	Placencia fishers start to leave fishing profession for tourism
1989	Friends of Laughing Bird Caye (FOLBC) was created
1990	Placencia Cooperative did not produce ice due to malfunction of electrical generators
	Placencia Cooperative’s profits from conch and lobster crashed

Table A.2.2. Continued

Year	Socio-Ecological Event
1991	Government of Belize declared Laughing Bird Caye National Park
1993	Belize Electricity Limited began to supply 24-h electricity to Placencia
1996	Regional marine conservation movement initiated in the Gulf of Honduras (GOH) with the creation of the Trinational Alliance for the Conservation of the Gulf of Honduras (TRIGOH)
1998	The Nature Conservancy (TNC) started monitoring fish spawning aggregations (FSAs) at Gladden Spit
	Hurricane Mitch (Category 4) impacted the Gulf of Honduras
2000	Government of Belize declared Gladden Spit and Silk Cayes Marine Reserve
	Hurricane Keith (Category 4) impacted Belize
2001	Hurricane Iris (Category 4) impacted Placencia directly
	Belize National Spawning Aggregation Working Group was created
2002	FOLB became Friends of Nature (FON)
	Formal co-management of GSSCMR started
2003	Government of Belize created 11 Marine Reserves around FSAs
2006	FON formally replaced TNC in the monitoring of FSAs at GSSCMR
	FON issued special fishing licenses for fishing mutton snapper at Gladden Spit for the first time
2007	Placencia airstrip was paved and renovated
2009	FON became the Southern Environmental Association (SEA)

A.2.3. Summary of fishery-dependent and fishery-independent data estimated between 1999 and 2011 for the mutton snapper (*Lutjanus analis*) fishery at Gladden Spit, Belize. With exception of 2011, estimates were derived from SEA's electronic database. Field surveys were conducted in 2011 for this study. Landings surveys were not conducted in 2005 and 2010; data were missing from SEA's database for 2002.

Year	1999	2000	2001	2003	2004	2006	2007	2008	2009	2011
Annual landings estimates										
Total fishing effort (boat-d-fishing)	25	22	47	45	32	81	49	113	83	129
Total catch abundance (No. of fish)	390	772	1,117	853	962	1,375	910	3,296	3,042	5,037
Total catch weight (kg)	1,386	2,417	4,246	2,525	2,814	4,282	3,233	7,983	7,806	12,311
Sex ratios (M:F)	0.9:1	1.3:1	1.2:1	1.4:1	1.6:1	0.9:1	1.1:1	1.2:1	1.2:1	1.2:1
May landings estimates										
Daily number of boats landing (mean)	3	5	7	3	3	4	5	6	6	7
[range]	[2-5]	[4-6]	[4-8]	[2-5]	[1-4]	[2-9]	[3-5]	[3-8]	[4-8]	[3-10]
Total fishing effort (boat-d-fishing)	13	16	42	13	22	47	44	82	62	73
Total catch abundance (No. of fish)	222	704	1,023	110	819	922	827	2,349	1,900	2,584
Total catch weight (kg)	762	2,234	3,958	382	2,165	2,355	2,725	4,500	5,202	7,034
May sex ratios (M:F)	0.9:1	1.2:1	1.2:1	1.3:1	1.3:1	1.2:1	1.1:1	1.2:1	1.2:1	1.3:1
Peak UVC counts (No. of fish)	500	500	500	3,000	2,500	8,000	7,000	4,000	6,500	7,000

A.2.4. Summary of mutton snapper (*Lutjanus analis*) fishery data collected during landings at Buttonwood Caye, Belize, between March and June 2011. Catch per unit effort (CPUE) was estimated from landings by numbers (CPUE-Abundance) and by weight (CPUE-Weight).

Variable	March	April	May	June
Fishing fleet data				
Mean [range] number of boats fishing daily at Gladden Spit	3 [1-6]	5 [2-10]	15 [1-23]	7 [2-12]
Mean [range] number of boats landing daily at Buttonwood Caye	4 [1-7]	4 [1-9]	9 [1-15]	6 [2-9]
Mean daily proportion of boats surveyed at Buttonwood Caye (%)[1]	95	69	63	76
Number of different fishing boats in monthly landings[2]	7	9	19	11
Landings data				
Fishing effort by boat (boat-d-fishing)	39	25	73	31
Fishing effort by fisher (hook-h)	820	518	1,324	521
Catch abundance (number of fish)	10	416	2,584	2,037
Catch weight (t)	0.03	1.3	7.1	3.9
CPUE-Abundance (fish*hook-h^{-1})	0.01	0.8	2.0	3.9
CPUE-Weight (kg*hook-h^{-1})	0.03	2.6	5.3	7.6
Sex ratio (F:M)[3]	1:1.3	1:1.3	1:1.3	1:1.3

[1]Proportion of boats surveyed at Buttonwood Caye relative to boats recorded at Gladden Spit
[2]Fishing boats included 2-3 fishers on board
[3]Ratio of the monthly abundance of females to the monthly abundance of males

A.2.5. Species composition of the bycatch from the mutton snapper (*Lutjanus analis*) fishery in landings at Buttonwood Caye, Belize, between March and June 2011. Species are listed in order of numerical abundance. Common names follow Froese and Pauly (2012), species names follow Eschmeyer and Fricke (2012). The mean TL (mm) and mean TW (kg) of the 15 most abundant species are indicated in parentheses. Percent bycatch is calculated from the number of individuals for each species, relative to the total number of individuals landed as bycatch (18,709). Raw species richness (%) is the percentage of the number of bycatch species in monthly catches relative to the total 49 bycatch species landed during the sampling period.

		TL; TW	Number of individuals landed				Total	%
Common name	Species	(mm; kg)	March	April	May	June	number	bycatch
Yellowtail snapper	*Ocyurus chrysurus**	(403; 0.8)	15752	222	6	28	16,008	85.6
White grunt	*Haemulon plumierii*	(275; 0.5)	292	65	0	2	359	1.9
Blue runner	*Caranx crysos*	(473; 1.5)	0	41	23	294	358	1.9
White margate	*Haemulon album*	(480; 0.7)	265	0	0	0	265	1.4
Yellowfin mojarra	*Gerres cinereus*[b]	(310; 0.2)	185	0	0	0	185	1.0
Lane snapper	*Lutjanus synagris*	(335; 0.7)	4	168	0	0	172	0.9
Queen triggerfish	*Balistes vetula*[b]	(487; 1.5)	142	8	1	20	171	0.9
Schoolmaster	*Lutjanus apodus*	(346; 0.8)	147	5	3	0	155	0.8
Saucereye porgy	*Calamus calamus*	(290; 0.5)	144	5	0	0	149	0.8
Bluestriped grunt	*Haemulon sciurus*	(260; 0.2)	120	3	0	0	123	0.7
Red hind	*Epinephelus guttatus**[b,i]	(177; 0.7)	43	24	21	7	95	0.5
Dog snapper	*Lutjanus jocu**[b,p]	(564; 4.8)	55	8	15	14	92	0.5
Longjaw squirrelfish	*Neoniphon marianus*	(150; 0.2)	86	0	0	0	86	0.5
Cubera snapper	*Lutjanus cyanopterus**[b,p]	(766; 7.7)	0	12	26	35	73	<0.5
Coney	*Cephalopholis fulva*	(180; 0.5)	62	3	0	0	65	<0.5
Ocean triggerfish	*Canthidermis sufflamen*[b]		9	12	12	23	56	<0.5
Rock hind	*Epinephelus adscensionis**[b,i?]		49	5	0	2	56	<0.5
Great barracuda	*Sphyraena barracuda*[p]		15	10	7	10	42	<0.5

Table A.2.3. Continued

Common name	Species	TL; TW (mm; kg)	Number of individuals landed March	April	May	June	Total number	% bycatch
Black grouper	*Mycteroperca bonaci**[,p]		3	14	11	5	33	<0.5
Greater amberjack	*Seriola dumerili*[p]		6	23	4	0	33	<0.5
Horse-eye jack	*Caranx latus**[,p]		2	4	2	9	17	<0.5
Rainbow runner	*Elagatis bipinnulata*		0	0	0	13	13	<0.5
Black durgon	*Melichthys niger*[b]		11	0	0	0	11	<0.5
Bar jack	*Carangoides ruber**		1	2	0	6	9	<0.5
Graysby	*Cephalopholis cruentata*		9	0	0	0	9	<0.5
Little tunny	*Euthynnus alletteratus*		0	0	8	0	8	<0.5
Yellowfin grouper	*Mycteroperca venenosa**[,p]		0	0	2	6	8	<0.5
Crevalle jack	*Caranx hippos**		4	1	1	1	7	<0.5
Black snapper	*Apsilus dentatus*		0	0	6	0	6	<0.5
Spanish makerel	*Scomberomorus maculatus*		1	0	0	5	6	<0.5
Red grouper	*Epinephelus morio*		3	1	1	0	5	<0.5
Doctorfish	*Acanthurus chirurgus*[b]		2	0	0	2	4	<0.5
Nassau grouper	*Epinephelus striatus**		0	2	0	1	3	<0.5
Porkfish	*Anisotremus virginicus*		3	0	0	0	3	<0.5
Bermuda chub	*Kyphosus sectatrix*[b]		3	0	0	0	3	<0.5
Black margate	*Anisotremus surinamensis*		0	2	0	0	2	<0.5
Tiger grouper	*Mycteroperca tigris*[*]		0	2	0	0	2	<0.5
Blackfin snapper	*Lutjanus buccanella*[p]		0	0	2	0	2	<0.5
Cobia	*Rachycentron canadum*[b]		1	1	0	0	2	<0.5
Remora	*Remora remora*[b]		2	0	0	0	2	<0.5
Blacktip shark	*Carcharhinus limbatus*[b]		2	0	0	0	2	<0.5
Lionfish	*Pterois spp.*[e]		0	0	2	0	2	<0.5
Gag	*Mycteroperca microlepis*[c]		0	1	0	0	1	<0.5

Table A.2.3. Continued

Common name	Species	TL; TW (mm; kg)	Number of individuals landed March	April	May	June	Total number	% bycatch
Gray snapper	*Lutjanus griseus*		0	1	0	0	1	<0.5
King mackerel	*Scomberomorus cavalla*[p]		0	0	0	1	1	<0.5
Ocean surgeonfish	*Acanthurus bahianus*[b,c]		0	0	0	1	1	<0.5
French grunt	*Haemulon flavolineatum*		1	0	0	0	1	<0.5
Sailors choice	*Haemulon parra*		1	0	0	0	1	<0.5
Nurse shark	*Ginglymostoma cirratum*[b]		1	0	0	0	1	<0.5
	Total		17,426	645	153	485	18,709	
	Number of species in monthly catches		34	27	19	21		
	Raw species richness (%)		69.4	55.1	38.8	42.9		

*Species reported to aggregate to spawn at Gladden Spit (Heyman, 2001; Heyman and Kjerfve, 2008)

[b] Noncommercial species; used for bait or personal consumption at fish camp

[c] Species reported to aggregate to spawn in the Caribbean (Domeier and Colin, 1997) but not at Gladden Spit

[e] Exotic invasive taxa

[i] Landed individuals with mean TL<L_m (mean length at first maturity for the species) as reported by Froese and Pauly (2012); otherwise, mean TL>L_m

[i?] L_m unknown for species, probably immature

[p] Species with reputation for ciguatera poisoning and with no commercial value, as recounted by fishers

A.2.6. Summary of the biological variables measured for individual mutton snapper (*Lutjanus analis*) landed at Buttonwood Caye, Belize, between April and June 2011. Estimations were restricted to measurements collected between -1 and 7 days relative to full moon (drfm, with -1 indicating 1 day before full moon, 0, the day of full moon, and positive numbers, days after full moon) every month.

Variable		Month	
	April	May	June
Mean (± SE) TL (mm)	564.3 ± 4.1	544.5 ± 1.8	484.9 ± 1.6
Mean (± SE) TW (kg)	3.2 ± 0.07	2.7 ± 0.03	1.9 ± 0.02
Mean (± SE) age	5.69 ± 0.03	5.38 ± 0.04	3.87 ± 0.02
Mean (± SE) female GSI[1] (%)	3.6 ± 0.2	4.1 ± 0.1	2.3 ± 0.1
Mean (± SE) male GSI (%)	2.2 ± 0.1	2.6 ± 0.1	2.7 ± 0.2
Proportion (%) of females in gonad state[2]:			
Type I	34.4	39.3	66.4
Type II	20.0	31.4	12.2
Type III	43.9	29.1	21.4
Type IV	1.7	0.2	0
Proportion (%) of males in gonad state:			
Type I	10.3	30.1	22.3
Type II	89.7	69.9	77.7
n (fish)	403	2375	1872

[1] Gonadosomatic index (GSI): the proportion between individual gonad weight (GW) and total body weight (TW) used to indicate gonad development and estimated as GSI=(GW/(TW-GW)*100)

[2] See text for description of gonad state

A.2.7. GIS data available for Belize and derived layers for spatial analyses in this study. Data were collected from Burke and Sugg (2006) and BERDS (2008).

Data category	Format	Derived project layers
Ecosystems of Belize	Vector	1) Major marine habitats of Belize 2) Marine protected areas (MPAs) of Belize 3) Management status of the MPAs 4) Fisheries management status of MPAs
Topography and bathymetry of Belize	Vector	5) Hydrological boundaries of study area
Catch per unit effort (CPUE) of commercial fisheries across Belize	Vector	6) Fishing pressure gradient (CPUE)
Mesoamerican Barrier Reef (MBR) Watershed	Vector	7) Individual river discharges (volume) 8) Hydrological basins (> 50 km^2) 9) Sediment loads to coastal lagoons
Continent and political limits	Vector	11) Country boundaries
Patch and barrier coral reef	Vector	12) Not geoprocessed

A.2.8. Solution to the pairwise comparison matrix (CR = 0.07). The eigenvalues are the relative weights of factors in the weighted-linear-combination equation. Eigenvalue weights were calculated using the WEIGHT decision support module in Idrisi-Andes.

	MHT	DSA	CPG	FPG	Eigenvalue weight
MH	1				0.5558
SD	1/2	1			0.2665
CP	1/5	1/3	1		0.1101
FP	1/9	1/7	1/2	1	0.0676

MHT: marine habitat type
DSA: distance from spawning aggregations sites
CPG: continental pollution gradient
FPG fishing pressure gradient

A.2.9. List of snapper species (family Lutjanidae) that were identified in juvenile stage (TL<100 mm) along 648 underwater belt transects across the southern Belize shelf and surveyed in March and July 2009. Four species (*) spawn in multi-species spawning aggregation sites along the Belize Barrier Reef (Heyman et al., 2005; Heyman and Kjerfve, 2008; Kobara and Heyman, 2010). Species are listed in order of numerical abundance. Common names follow Froese and Pauly (2012), species names follow Eschmeyer and Fricke (2012).

Common name	Species	n
Schoolmaster	*Lutjanus apodus*	629
Gray snapper	*Lutjanus griseus*	143
Dog snapper*	*Lutjanus jocu*	124
Yellowtail snapper*	*Ocyurus chrysurus*	58
Lane snapper	*Lutjanus synagris*	38
Mutton snapper*	*Lutjanus analis*	10
Mahogany snapper	*Lutjanus mahogani*	4
Cubera snapper*	*Lutjanus cyanopterus*	1
	TOTAL	1,007